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Biological Sonar Systems

a bionics survey

Texas University

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BIOLOGICAL SONAR SYSTEMS: A BIONICS SURVEY

FINAL REPORT UNDER CONTRACT N00024-68-C-1339, ITEM 25
1 November 1971 - 31 August 1972

NAVAL SHIP SYSTEMS COMMAND
Contract N00024-68-C-1339,
Proj. Ser. No. S2616, Task 12867

K. Jerome Diercks

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13 ABSTRACT

The literature on biological sonar systems (bats, birds, marine mammals) was reviewed and past and present investigators were interviewed to ascertain the contributions, present and potential, of work in this field to high resolution sonar technology. It was concluded that there have been no contributions to date. Five areas of research were identified as potentially contributory: passive target ranging by the owl, signal design for target recognition, neural processing for target detection and recognition, the psychophysiology of sound localization, and the mechanics of signal generation by the small whales. The available system(s) and performance data on the bats and small whales are tabulated, and up-to-date bibliographies on each biological order are included.(U)

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I. INTRODUCTION

Applied Research Laboratories (ARL), The University of Texas at Austin, under Contract N00024-68-C-1339 with Naval Ship Systems Command, has performed a survey of bionics research on animal sonar systems. Funding for this work began 1 November 1971 and terminated 31 August 1972. This report describes the nature and scope of this effort and summarizes the conclusions reached.

The objective of this effort was to identify and specify the features of biological sonar systems which can be exploited by sonar technology or the knowledge of which might influence or alter sonar design philosophy. The biological forms considered in this survey are the insect-eating bats (Order Chiroptera; Suborder Microchiroptera), whales, dolphins, and porpoises (Order Cetacea, Suborder Odontoceti), and a few species of birds.

The literature relating to biosonar systems was reviewed. Nearly 600 documents relating to echoranging, physiological mechanisms of sound generation and reception, morphology, and ecology (diet, habitat, etc.) were collected. Included are approximately 85 foreign language reports (44 in Russian, 24 in French, and 17 in German) which are being translated (45 completed to date). A tabulation of data for each bioform is included in the appendices. Bibliographies of the documentation on biosonar systems are also included.

Most active members of the biosonar community and many members of the sonar engineering community at ARL were interviewed to achieve a critique of bionics research. A listing of the biosonar membership contacted is included as Appendix I. A standardized questionnaire was employed to guide the discussions, namely:

(1) Has bionics research on animal sonar systems contributed to synthetic sonar design or design philosophy? In what ways?

(2) What areas of animal sonar research appear most likely to provide guideline information for synthetic sonar design or design philosophy?

(3) In what ways can sonar engineering aid bionics research on animal sonar systems to derive guideline information for sonar technology?

The answer to the first question was unanimously, no. The answer to the second question is the principal topic of this report. There were two answers to question 3. The first, explicitly stated, was to provide improved instrumentation (broader bandwidth, greater sensitivity) for detection, recording, and analysis of biosonar signals. The second, implied, was to communicate the interests and requirements of sonar technology to provide guidelines for productive biosonar research. Apparently, previous attempts to achieve the latter--whether initiated by the engineer or biologist--have been essentially unsuccessful.

There are several excellent, comprehensive reviews of biosonar phenomena (Refs. 4,41,44,70,91,107,120,122,131,147,164,170,175), and this report will not attempt to reiterate these. Five broad categories of bionics information are identified: target detection phenomena, target classification phenomena, signal processing for detection and classification, passive/active sonar utilization, and mechanisms for sound generation and reception. The first two will be considered together.

II. TARGET DETECTION AND CLASSIFICATION PHENOMENA

Sonar technology stands in awe of the apparent ease with which biosonar systems detect and classify targets. In many instances the operating sonar/target parameter relationships significantly exceed those achieved by synthetic means. For example, bats are able to detect and avoid wire obstacles in their flight path at wavelength-to-target diameter (λ/d) ratio values of 15 to 25 (Refs. 48,49,53,63, 66,84,98,140,158). Food prey, like gnats and mosquitoes, yield ratio values of 1 to 10, depending upon the target dimension selected. The dolphin readily finds objects 0.25 to 0.5λ in dimension (Refs. 74,78) and avoids obstacles 0.1λ in dimension (Refs. 26,27,77,78,111). It is reported able to resolve* targets separated 1 to 2 mm (0.05 to 0.1λ) in range and 0.25° to 1° in azimuth (Ref. 5). The owl determines bearing <u>and apparently range</u> passively and suffers but slightly doing so with only one receiver (ear) (Ref. 79,125).

Members of both biological orders have been trained to discriminate between 2- and 3-dimensional targets of differing shapes, forms, and materials (Refs. 6,17,38,54,67,78,81,83,145,146,152,168). Once the animal comprehends the task requirement, identification of a positive (versus any other) target by echolocation (Refs. 81,83,128,135), discrimination performance improves relatively rapidly. That is, the animal readily learns (identifies) characteristics of the target echo that identify the positive target (and <u>in absentia</u>, also identify any negative target). It has been necessary to "teach" some dolphins to echolocate in a testing environment (Refs. 3,16,109), but once "taught" they perform (discriminate between targets) as well as any other so tested. The limits of ability to discriminate size (acoustic cross

*It is probable that the animal is detecting qualitative differences between the echoes from the test targets and a single target presented simultaneously without actually measuring (resolving) the separation between the test targets.

section, or target strength) have been determined for several species (Refs. 3,17,41,128,157). A working value is 10% difference in size (Refs. 3,113,152) or 1 dB difference in target strength (Refs. 41,128).

The detection/avoidance phenomena imply apparent operation in a low noise background (at least within the requisite bandwidth, whatever that might be), or the ability to process the echo signals to achieve an effectively high signal level (or low noise level), or probably both. Attempts to mask echolocation by projecting high intensity, broadband noise into the flight path of bats have been only partially successful (Refs. 50,53,60). It appears there is a physiological signal-to-noise ratio greatly exceeding the physical value, and knowledge of how this is accomplished would assuredly benefit sonar technology. Current efforts in electrophysiological biosonar measurements are rapidly increasing our understanding of the mechanisms involved and should be supported (see next section).

A "figure-of-merit" (Ref. 44) calculated for a post World War II search radar, for two species of FM bats, and for a dolphin yields comparable performance values for the bats and the radar (Ref. 44), but indicates the dolphin is several orders of magnitude poorer (Ref. 137). However, the latter result is questionable due to poor validity of the measurements assumed in performing the calculation.

The owl's ability to localize <u>and range</u> passively, insofar as it is documented and understood, is of prime interest to the sonar community, and increased support of efforts aimed at understanding this ability is highly recommended.

In most parameters, synthetic sonars excel their biosonar counterparts. The exceptions are in bandwidth and signal-to-noise ratio. Recent developments in sonar technology indicate a capability of achieving comparable bandwidths (Refs. 14,34). Detection and classification, then, seem not to be a question of capability, but of ability. A design philosophy which specifies mechanical processing of echoes precludes a legitimate comparison with biological systems. They are not comparable at this time. Sonar technology has achieved only marginal success with wholly mechanical systems, regardless of their capabilities. Knowledge of biosonar capabilities and abilities thus begs the recommendation that the ear-brain processor (the sonar operator) be reintegrated into sonar evaluation philosophy.

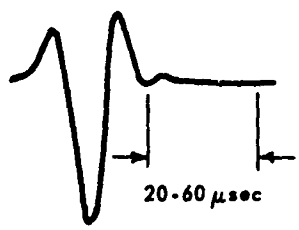
Little is known about echolocation by whales in the wild. They are intelligent and curious, and the observer's presence assuredly alters their behavior and stimulates acoustic activity probably more excitatory than echolocational in nature. Bats, however, seem little bothered by the presence of man in their environs and may be observed without disturbing their normal behavior. Some bats capture as many as 15 to 25 insects per minute under natural conditions (Refs. 51,118), but in the laboratory must be trained to discriminate (i.e., be provided experience with) non-food objects. They will attack any object from pebble size to basketball size the first few times it is thrown into their flight path (Ref. 62). (After training, especially when satiated, bats will often attack these non-food objects, apparently for diversion (Ref. 164).) A dolphin that has been trained to discriminate artificial (non-food) targets and has been fed whole dead fish, which it sometimes must retrieve acoustically, will ignore a similar specimen when presented as a target object in a testing environment (Ref. 10). Thus, it appears that routine classification is "monopolar" and intrinsic to the context in which it is performed. For instance, an echo indicates a likely food object, or positive target, and therefore initiates pursuit or approach, or it doesn't. In the wild echolocating animals, such as bats, may actively classify little more than surface, whether it is land or water (Refs. 46,121). The insectivorous bat in a hunting context pursues any object in translational motion. (It does not attack rustling leaves, and it soon learns that not all "flying" objects are food.) The dolphin learns to recognize, and to respond to, an echo signature in context and to ignore it out of context.

This consideration suggests a fundamental guideline for bionics research, that is, to vary the animal's sonar problem and monitor the development of its solution rather than to evaluate the apparent solution after it has developed, which is the usual practice. This will allow description of the testing procedure (the signal design) employed by the animal to achieve a solution. Then, with knowledge of the target(s), it would be possible to provide a description of the problem and, thus, its solution. The merit of this procedure is universally recognized, but it has not been practiced for perhaps obvious reasons. An operational criterion for inferring the existence of olution is the stabilization of behavior. It is then a simple matter to record a short sequence of measurements after this criterion is reached. The alternative is to record many measurements over an indeterminate period during development of the solution, and the cost may be excessive. However, the former approach yields no way of knowing if the apparent solution is optimal, a consequence of adaptive testing within the constraints of the animal's capabilities, or is merely effective, a manifestation of the only overt solution the animal is capable of, regardless of the problem. From the viewpoint of sonar technology, the potential return from a "developmental" approach would seem to more than offset its probable cost.

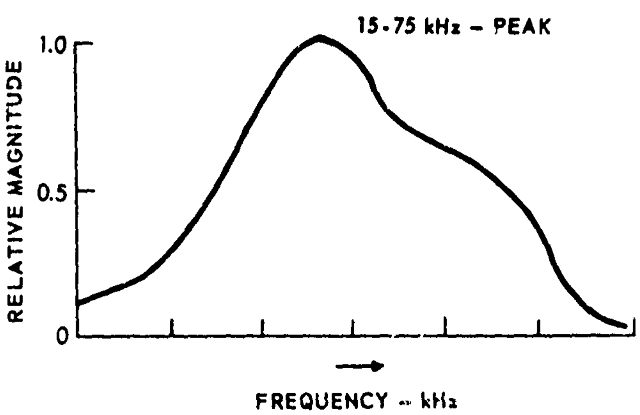
A second alternative is to continually vary the sonar problem, by substitution or replacement of targets, once it has been established that the animal understands what it is required to do, and to monitor the changes in the animal's echolocation behavior, which are then corollated with the assumed changes in the problem (Ref. 146). The dangers of this procedure are that the animal may fail to understand the behavior required of it and cease to perform, or that it may proceed with the overt behavior of the testing paradigm without performing any acoustic discriminations (Ref. 10). Any conclusions drawn from this latter event would be most misleading. However, use of this technique has illuminated apparent differences in the signals employed by one species of FM bat for "orientation," "target location," and "classification" (Refs. 146,152).

The small whales use a transient-like, usually ultrasonic click for echolocation (Refs. 12,13,41). This is a broad bandwidth signal: 3 to 5 octaves, $Q \approx 1$. The generic form is illustrated in Dwg. AS-72-923. The mechanism of generation is moot (see Section IV on mechanisms of sound generation). The signal is directed forward in a narrow, conical beam (20° to 90° beamwidth, depending on frequency) (Refs. 39-41,112,138,139,170). Signal frequency decreases with angle from the acoustic axis (Refs. 34,112), a feature which may be exploited for target localization and/or classification. The dolphins scan the forward volume (direction of motion) by rotating the head through an elliptical path (up-and-down as well as side-to-side motion) (Refs. 41, 111,112,128,170). It is not known whether this is related to transmission, reception, or both.

Whales employ a somewhat stereotyped transmission format for echolocation of artificial targets in a tank (Refs. 13,38,41,74, 101,113,128). As the animal closes range on the target(s), it transmits usually at an increasing rate and reduces signal intensity. There is no ambiguity; the next transmission occurs only after receipt of the echo from the preceding transmission (Ref. 101). The generator may, in fact, be triggered by feedback from the receiver, although experienced test animals seem able to consciously control repetition rate, transmitting only often enough to maintain tracking and/or to achieve target identification (~ 25 to 50 per second) (Ref. 10). Signal intensity is reduced, apparently to minimize extraneous returns from other targets or surfaces. The dynamic range of intensities over



WAVEFORM



SPECTRUM

GENERIC DOLPHIN ECHOLOCATION SIGNAL

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a 3 to 5 m test path is greater than 35 dB (exceeds the range of available recording ins ruments). No reliable spectral changes have been observed over this distance (Refs. 12,13,135).

Bats use a diversity of signal forms for echolocation: short duration (1 to 5 msec) frequency modulated (FM) slides (Refs. 48,61, 65,118,130,145,146,149,161,168); long duration (20 to 100 msec), constant frequency (CF) bursts, terminated with a short duration FM slide (Refs. 1,61,65,85,116,141,142,172); a mixed form consisting of a short duration CF burst terminated with a similar duration FM slide (Refs. 61,65,117-119,124,157); and short duration (~1 msec) CF pulses (Refs. 48,98). (One species of Megachiropteran bat, Rousettus aegypticus, generates an audible transient by clicking its tongue (Refs. 49,87).) Signals may be pure (Refs. 48,65,97,130,147,149) or contain one or more higher harmonics (Refs. 48,61,65,116,118,130, 140,142), one of which may dominate (Refs. 61,65,118,130,140,142). FM bandwidths range from about 0.2 to 2 octave, depending upon species (Refs. 48,116,118,130,145,146,149,173), signal form (Refs. 61,65,85,130), and phase of pursuit/capture or obstacle avoidance maneuver (Refs. 145, 146,157,158,168). Sounds are generated in the larynx (see Section IV on mechanisms of sound generation). The FM bats radiate through the open mouth, which is formed like a megaphone. The directivity pattern is broad (~45° to 90° at the half-power points)(Refs. 92,148,155), but the sound field is frequency structured and it is thought that bats achieve fine spatial resolution by exploiting this feature (Ref. 64). They do not appear to scan mechanically during pursuit/tracking (Ref. 167).

The CF bats in general radiate through the nostrils, which are separated by one-half wavelength at the dominant frequency and may be enclosed in a tissue appendage (nose leaf, horseshoe) which aids in directing the transmission (Refs. 44,92,95,97,98,100,131,154,172).

Directivity is greater than for FM bats (beamwidths about 30° to 60° at the half-power points)(Refs. 92,97,100,141,148,154,156), and there is noticeable mechanical scanning of the head during pursuit/tracking (Refs. 69,94,95,97,100,142).

Bats also employ a stereotyped transmission format. When searching they pulse at a low repetition rate (5 to 10 per second). Analogous to synthetic sonar usage, this may indicate an ability to detect at much longer ranges than ordinarily attributed to these animals (Ref. 46) or it may be merely a manifestation of energy conservation (Ref. 44). During pursuit/capture or obstacle avoidance, the repetition rate increases and signal intensity is reduced (Refs. 6,28,44,45,51,69, 82,85,117,119,124,140,141,145,146,157,161). It is moot whether the onset of increased pulse repetition indicates the time of detection, classification, or merely initiation of pursuit. It is not unlikely that detection/classification occurs during search, perhaps aided by passive clues (Refs. 6,82,162) and possibly vision (Refs. 1,2,22,29, 102,159). The FM bats initiate pursuit or avoidance at about 1 to 3 m distance from the target (Refs. 6,21,51,54,63,119,157,158), and the CF bats at about 3 to 10 m distance (Refs. 97,99,124).

The FM bats shorten the duration of their signals during pursuit/avoidance to prevent pulse-echo overlap, except in the final moments of capture, and they reduce the frequency range of their slides by successively omitting the higher frequency components (Refs. 28,45,51,145, 157,168). Thus, resolution is progressively degraded (directivity and bandwidth are reduced) during pursuit/capture. Some species emit pulses in doublets during the later stages of pursuit/avoidance (Refs. 98,161). The intent of this change in transmission format is unknown.

Bats transmitting a mixed signal form follow the same protocol, except the signals are first shortened by eliminating the CF portion, then proceed as do the pure FM species (Ref. 157).

The CF bats permit pulse-echo overlap throughout the pursuit/avoidance maneuvers (Refs. 117,122,124,141). Some species shorten signal duration during target closure to maintain constant pulse-echo overlap (Refs. 117,119,122). The benefit derived from this is unknown.* Other species initially increase the duration of their transmissions to increase pulse-echo overlap, then proceed by shortening the duration more or less linearly with range to keep the FM ending of the echo constant in time relative to the onset of the transmission (Refs. 117,122). The lengthy overlap probably permits accurate determination of the Doppler shift in echo frequency resulting from platform (bat) motion.** The benefit derived from initially increasing overlap and then maintaining the relationship described is, again, unknown. Initial pulse-echo overlap may index detection. Increasing the overlap might then facilitate the initiation of pursuit at the earliest time (greatest target distance). The *Rhinolophidae*, the horseshoe bats, emit a long CF pulse during search, but change to a short pulse burst transmission mode when approaching an obstacle (Refs. 45,52,85,140-142). Both the search and burst pulses terminate with an FM sweep (Refs. 45,85, 141,142). It is speculated the intent of this change in signal format is to increase the rate of information provided by the terminal FM portion of the echo. This interpretation seems overly simple. The total duration of a pulse burst is usually longer than a single long pulse (Refs. 85,140-142);pulse echo overlap is thus increased with no apparent synchrony between pulses and echoes. The bat may be able to attend to only the FM portions of the signals and thereby achieve some resolution. But then why does it emit the CF portion of the signal

*It is possible the overlap generates a difference-frequency component which signals the generator to stop transmitting; i.e., the duration of overlap is a measure of the system's reaction time. The bat senses target closure by apperception of the shortening of signal duration.

**Sensing of constancy of frequency shift may be apperceived as normal progression of target closure.

at all in this mode? These bats excel the FM species in detecting smaller obstacles at longer ranges (Refs. 84,85,124,140,141); accordingly, their sonar merits additional study.

There are no outstanding singular differences between the sonar problems confronting FM and CF bats, as manifested by their hunting behavior(s), diet(s), and ability to resolve artificial targets in the laboratory (Refs. 46,49,84,116,120,158,163). Both feed on flying insects; the CF bats, being somewhat larger in size than the FM bats, often attack larger species (Refs. 44,163,164). The CF bats are less agile flyers than some of the FM species and are able to hover in flight, which allows them to capture crawling or stationary prey (Refs. 98,120,162,163). The insectivorous bats, confronted with the problem of tracking small moving targets in an uncluttered environment, emit high intensity signals (SPL ~135 dB re 0.0002 dyne/cm^2 at 10 cm), while the hovering bats, seeking large or motionless prey in oftentimes dense foilage, emit relatively low intensity signals (SPL ~75 dB re 0.0002 dyne/cm^2 at 10 cm) (Ref. 43). The fishing bat, Noctilio leporinus, which is sometimes insectivorous, emits a relatively intense signal (Ref. 48). Many of the CF bats achieve a broad signal bandwidth by emitting many harmonics, but in an ill-defined format (Refs. 48,118).

Noctilio using a mixed signal form is able to detect small perturbations of the water surface to locate fish swimming just underneath, which it then gaffs with its feet (Refs. 20,120,157). It is able to detect small wires protruding above a smooth water surface (Ref. 157), as well as the "wake" of a fish traversing a wind rippled surface (Refs. 20,44,120). During pursuit/capture it shortens its signal by successively eliminating the CF portion to prevent pulse-echo overlap (Ref. 157). It employs a different transmission format to detect and avoid wire obstacles in its flight path than it does to pursue fish. That is, it continues to transmit a mixed signal form throughout without shortening the pulse and uses pulse-echo overlap as it closes the target/obstacle (Ref. 158).

The megachiropteran bat, Rousettus sp., together with the South American Oilbird, Steatornis, and certain species of Asian Cave Swiftlets, Collocalia, emits click-like echolocation signals generated with the tongue and radiated from the corners of the mouth (Refs. 43,44,49,55,87,115). All utilize the capability functionally, in lieu of vision, for navigation or orientation in the dark; none apparently uses it for detection and pursuit of prey (Refs. 43,44, 49,96,102).

III. SIGNAL PROCESSING FOR DETECTION AND CLASSIFICATION

Available evidence indicates that an animal's signal characteristics are matched to its receiver capabilities (hearing) (Refs. 5,30,41,57,61,65,68,70,75,86,103,162). Hearing sensitivity changes as the animal matures, and it apparently adapts its signal form to coincide with these changes (Ref. 65). After maturation there is evident adaptation to changes in sonar environments and/or tasks (Refs. 1,2,21,42,44,98,145,158,167).

There are few data relating directly to signal processing for target classification. The reason for this is principally procedural. Even when it is possible to monitor both the transmitted and target echo signals, as well as the animal's behavior, it is operationally difficult to ascertain the time of occurrence of, or to infer the analytic sequence leading to, a classification decision. There is sufficient signal-to-signal variation to generate quite misleading or erroneous conclusions should the improper moment or sequence be selected. Bat and dolphin signal forms have been mechanically simulated to examine echo characteristics of targets used in animal tests (Refs. 17,21,31,32,41,54,136,168,169). A study of target shape discrimination by the bat, Vampyrum spectrum, an FM bat, followed by analysis of target echoes generated by artificial signals, indicated learned discrimination based upon overall echo amplitude differences by one bat and upon frequency response differences by a second bat (Ref. 21). Other similar efforts have been noticeably less successful (Refs. 17,31,32,54,136,168,169). Correlations between identified echo signal characteristics and known target characteristics or between signal characteristics and the animal's discrimination performance are minimal and unreliable. Presentation of the data,

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translated in frequency to human listeners, results in facile discrimination of perceived signal characteristics that identify a class of targets (e.g., "hard," "soft," spherical, cylindrical) (Refs. 32,168). Attempts to extract these clues by machine processing have been only marginally successful (Ref. 12,31,32).

Analyses of signals emitted by dolphins during target shape and/or material discriminations have been generally unrevealing; the signals (emitted and/or reflected) examined do not exhibit significant differences in form or spectrum (Refs. 12,13,135). There is a reported correlation between discrimination performance and echo structure (of elastic targets) (Ref. 35), but this is not unexpected. Finally, it has been speculated that bats and dolphins utilize learned target motion behavior (track, range rate) as a (perhaps the) classification clue (Ref. 56).

There are abundant data relating to signal processing for target/echo detection and localization. The results to date are both exciting and encouraging. Electrophysiological measurements of activity in peripheral and higher nervous centers in response to artifically and self-generated sounds have revealed unique capabilities related to the echolocational process(es) of both bats (Refs. 6,57,58, 59,61,64,65,69,70,103,106,127,162) and dolphins (Refs. 23,24,88). Work in this area is expanding. By 1973 the recording of radio-telemetered data from free-flying bats with microelectrodes chronically implanted in the auditory nervous system should be accomplished (Ref. 71). Progress on analogous measurements on dolphins is hindered principally by state-of-the-art knowledge of animal maintenance and care.

The auditory systems of echolocating bats are sensitive to ultrasonic frequencies, maximally so in the region(s) of their emitted sounds (Refs. 5,30,57,61,65,103,106,127,162). Also, they are capable of fast time resolution, and some species show an increased responsiveness to the second of a pair of sounds (an "echo" after transmission) (Refs. 58,64,65). (Recent work on dolphins shows similar capabilities for those animals (Refs. 23,24).) Hearing sensitivity in those bats that transmit a relatively long duration, constant frequency (CF) signal is sharply tuned (effective roll-offs of several hundred decibels per octave change in frequency) to the dominant frequency emitted while the bat is at rest (Refs. 61,65,103,106,127, 151). In flight these bats lower their transmitted signal frequency to compensate for Doppler shifts in the echo caused by source and/or target motion and thus maintain the echo at the frequency of maximum hearing sensitivity (Refs. 127,141-143,151). This has the effect of reducing apparent echo masking during pulse-echo overlap (Refs. 103, 106,127,143) and of sharpening target localization by rejection of off-axis target echoes, which will be shifted less in frequency (proportional to the cosine of their angle with the acoustic axis) than those on-axis (Refs. 103,143). Apperception of the shift in signal frequency would yield a measure of range rate.

All species, CF and FM, reduce signal intensity during target closure, probably to minimize echo clutter (volume reverberation) from extraneous targets (Refs. 44,69,82,85,140,141,145,157).

The CF bats radiate sound from a dipole source* (the nostrils, separated one-half wavelength at their most sensitive frequency) and scan the sound beam by moving the head during echo ranging (Refs. 97, 98,142). They also move their pinnae (external ears) through a forward-to-side-looking arc while echolocating (Refs. 52,70,97,131-133,142). The pinnae alternate, one directed forward while the other is directed laterally. In the Greater Horseshoe bat, Rhinolophus ferrum equinum, the alternations occur in synchrony with the emitted pulses (Ref. 52). In other CF bats, the emission rate and ear movements are asynchronous (Refs. 69,70,133,142). The two scanning behaviors, projecting and receiving, together provide for crossrange (or azimuthal) tracking;

*Except Chilonycteris p. parnelii which emits through the open mouth.

the latter alone may provide for crossrange rate determination. It has also been speculated that the ear movements, by providing a Doppler scan across frequency, may facilitate accurate frequency tracking (Ref. 151). Also, by orienting one receiver toward the target and the other orthogonally to this direction, the animal enhances its ability to detect the target echo in a noisy environment (Ref. 60).

The short FM slide (~10 kHz) terminating each CF transmission may function as an alerting signal during searching behavior when the animal is at rest. If, when searching, the bat transmits at or near its frequency of maximum sensitivity, the CF portion of an echo will be shifted upward to a less sensitive frequency region. However, the FM part of the echo will sweep down through the region of maximum sensitivity and thus alert the bat to the presence of a target. The utility of this function would be vitiated in flight, unless target motion shifted the echo frequency above the region of maximum sensitivity.

There has been much recent speculation about the intent and use of the CF and FM portions of the signals emitted by the "CF" bats, and, in comparison with the "pure FM" species, of the capabilities inherent in the two generic signal forms (Ref. 174). It is conceded the FM bats use an optimally Doppler tolerant waveform for determining target range (Refs. 7,174). The CF bats presumably minimize the effects of Doppler shifts in echo frequency upon target range determination by compensating for these shifts during transmission of the CF portion of the signal, i.e., by sliding the signal up or down in frequency to compensate for Doppler. The FM portion of the echo is maintained at the same "frequency" as that of the transmission to yield minimum ranging error (Ref. 174).

Hearing sensitivity in the FM bats is broadly tuned to cover the range of frequency changes and in some instances is bimodal, showing increased sensitivity over the ranges of the first and second harmonics of the transmission (Refs. 5,30,57,61,65,162). These bats continuously reduce signal intensity during closure, presumably to minimize echo clutter from extraneous targets. They also shorten signal duration, to prevent pulse-echo overlap, and reduce FM bandwidth to about 15% of its initial (search) value during the pursuit/capture or obstacle avoidance maneuver (Refs. 45,51,54,145,146,168). Studies with two species of FM bats, the big-brown bat, _Eptesicus fuscus_, and the neotropical spear-nosed bat, _Phyllostomus hastatus_, have demonstrated the apparent use of correlational processing for range determination (Refs. 147,149). The test problem was seemingly unnatural for the bats; they were required to ascertain the range difference between fixed targets from a stationary perch. It is moot whether they rely on correlational processing during pursuit. The change in signal parameter values would continuously degrade the processing gain and resolution available, but this might be compensated for by the improvement in signal-to-noise ratio which accrues during closure.

Theoretical speculations on biological sonar phenomena are difficult to test; most are heuristic. The positive results obtained in the previously mentioned studies with _Eptesicus_ and _Phyllostomus_ are exceptional. More commonly, the applicability of a theory is called to question by demonstration of failure of occurrence of a requisite feature or event (Refs. 28,60,74,90,114,144,160) at the level of measurement. Claims of "solutions" to biological sonar problems (Refs. 7,8) are premature and pretentious; the problems have not yet been defined (Refs. 47,82,110,121,164-166), and the signal forms are not yet reliably known (Refs. 18,33,34). Such claims are merely statements of the capabilities and limitations of the signal form(s) examined, _given the processing employed_ (Refs. 7,8,41); that performed by the animal is unknown but may be inferred from results like those obtained in the _Eptesicus_ and _Phyllostomus_ studies.

The projected sound field of an FM bat will be frequency structured, at least to the extent that frequency decreases with azimuthal angle. Receiving directivity is frequency dependent in a complex way (Refs. 6,61,64,65), and it has been shown that, by sampling an echo at three (or more) frequencies within the swept band, bats could localize the source of an echo uniquely in the forward hemisphere (Ref. 64). It is possible the CF bats utilize the terminal FM portion of their signal similarly.

Attempts to derive possible target classification clues by machine processing of bat and dolphin signals, or bat-like and dolphin-like signal echoes from assorted test targets, have been disappointingly unrevealing (Refs. 12,14,31,32). Presentation of the same signals, suitably translated in frequency to the audio range, to human listeners exposes obviously perceptible signal differences which are not revealed by the processing applied (Refs. 14,31,32). It is generally conceded that no extant machine or machine processing technique yields a meaningful analog of ear-brain processing (Refs. 25,47,121,150).

IV. MECHANISMS FOR SOUND GENERATION AND RECEPTION

Bats generate sounds in their larynx,* which is anatomically different from that of other mammals (Refs. 96,123), apparently evolved for production of the short duration, high intensity, ultrasonic signals used in echolocation. Ultrasonic capability is achieved by operating the vocal membranes at relatively high tension (Ref. 123). (See also, Ref. 173). Of significance in the present context is the ability to produce the high intensity levels recorded (~110 to 130 dB re 0.0002 dyne/cm^2, or 35 to 45 dB re 1 μbar at 10 cm**), given the minuscule size of the generating organ(s). This is apparently accomplished by causing a large overpressure at the distal port of the larynx; air is then metered through the laryngeal orifice for the duration and at a rate appropriate to the task (phase of the pursuit/avoidance maneuver) (Ref. 123). The transmission pattern is cyclic and correlates with respiration (Refs. 44,131,140,143,161).

The mechanism(s) of sound generation by whales is moot (Ref. 170). Three hypotheses prevail. First is that the sounds are generated in the larynx and transmitted via the musculature in the nasopharynx to the base of the skull, then along the maxillae (rostrum) into the water (Ref. 129). This hypothesis is not supported by anatomical or physiological evidence (Refs. 109,114). The other hypotheses are similar in the

* The megachiropteran fruit bat, Rousettus, generates echolocation sounds by "clicking" its tongue.

** Correcting for directivity yields source levels 6 to 12 dB lower than the values stated.

location of the generator, the nasal plugs in the bony nares,* but differ in the mechanics of generation. In one theory sounds are generated by friction grating of the plugs against the opposing tissue; this is under muscular control (Refs. 37,39). The effect is either a staccato-like hammering of the skull, or cavitation as the plug moves, or both. The other hypothesis ascribes generation to flapping of the plug(s) against its opposing surface as air is metered past, much like a "bronx cheer" is generated with the lips (Refs. 108, 114). The effect here is, again, a hammering of the skull. Sounds are radiated via the fatty melon into the water, or along the maxillae into the water, or both.

The maxillae are apparently acoustically separated by cartilaginous tissue along most of their length (Ref. 37). Separation at the distal margin is nominally one-half wavelength at the peak signal frequency, implying a dipole source analogous to that described for the CF bats. Calculated directivity values for the bottlenose dolphin, Tursiops truncatus (Ref. 11), agree with measured values (Refs. 41,112), in support of the implied configuration of the radiator. Sound pressure levels ~110 to 130 dB re 1 μbar at 1 m have been reported for several species (Ref. 41). (However, see Ref. 170).

The amount of available information in an echo is dependent upon the bandwidth of the signal interrogating the reflector. The bandwidth of a whale's signal (see Fig. 1) greatly exceeds that of synthetic sonars and, hence, yields potentially more information about the nature of a target. Recent efforts to exploit this knowledge by mechanically simulating a whale-like signal for high resolution target classification (Ref. 14), while successful, have also illuminated the gross ineffeciencies of mechanical (electroacoustic) generation in comparison

*This location has been confirmed by acoustical measurements performed on the animal (Ref. 33).

with its biological counterpart. It is difficult to achieve the desired bandwidth <u>and</u> intensity <u>and</u> directivity simultaneously.

Accordingly, the mechanism(s) of sound generation and radiation by the odontocete whales would seem to be a promising area for bionics research, providing inputs to the fields of acoustics and sonar engineering. Support in this area is recommended. The bats' phenomenal sound producing capabilities, while intriguing to both the biologist and acoustician, do not present any basis for exploitation by sonar technology at this time.

Behavioral and electrophysiological evidence reveal that the auditory sensitivities of the bats and whales are not exceptional (Refs. 9,30, 57,61,65,68,72,73,75,76,86,126,162,171). The external meatus (ear canal) of the whales appears to be vestigial and the tympanic membrane (ear drum) nonfunctional (Refs. 19,88). The path of sound reception in the dolphin, *T. truncatus*, is via the posterolateral portion of the mandible (lower jaw) to the auditory bulla (Refs. 23,41,88,108,109). Stimulation is effected by differential vibration of the bulla and enclosed otic capsule (Refs. 88,109,134). The directional properties of the delphinid receiver are poorly known* (Refs. 23,88,111). There is some evidence these animals may be able to process separately the signals received on each side (Ref. 19,23,88). Other than its obvious utility for localization, the advantages of this apparent capability are moot.

The external ears of the bats are highly variable in relative size and form (Refs. 70,120,122,131,132). Their shape is often correlated with other behavioral or acoustic features. For example, many small-eared species are fast fliers and emit intense, high

* Measurements performed to date have all employed tone burst signals. Analogous data obtained using an echolocation-like click will probably differ somewhat from these.

frequency sounds. Other species that hunt resting or terrestial prey emit faint sounds and have relatively large pinnae. An external appendage, the tragus, located along the anterior margin of the external meatus, is prominent in many species (Refs. 70,131,132). Evidence indicates the function(s) of the pinna and tragus is to effect directional sensitivity; the pinna behaves as an attenuator to signals from undesired directions (rather than as an amplifier to sounds from the desired direction), and the tragus increases directional sensitivity in the vertical plane in some unknown fashion (Ref. 64).

Some species move their pinnae during echolocation, some synchronously with pulse emission, and others asynchronously. The purpose of this movement is unknown (see previous section on signal processing). Other species show no apparent ear movements. Directional sensitivity is a complex function of frequency and is dependent upon the shape and orientation of the pinnae. Bilateral symmetry apparently prevails. It seems likely the FM bats exploit the interaction between signal bandwidth and directional sensitivity to localize a target in three-dimensional space (Ref. 64). The CF bats could exploit the FM tail of their signals similarly. It is concluded that frequency/intensity differences between the ears are probably the determinants of sound localization (Refs. 59,97,132). At high signal frequencies directivity is of the order of 0.75 dB/° (Ref. 59). Intensity differences of 0.5 to 0.75 dB are discernible (Ref. 57). Thus, it appears that bats should be able to localize objects to within 1° (or less), at least within the conus of radiation.

Owls are characterized by asymmetry in the location of their external auditory meatuses on the head (Ref. 79,107,125); a line connecting their "acoustic centers" makes an angle of 10° to 15° with the horizontal. Directional sensitivity is a complex function of frequency* (Refs. 79,107,125). The asymmetry and directional sensitivity interact to permit accurate (and apparently unique) localization of a radiating source in the frontal hemisphere (Refs. 79, 107,125). Upon first detecting a sound in darkness, the owl turns its head toward the source. Once it faces the source, it must hear one additional sound before striking (Ref. 125). Thus, the owl must apparently face the source "directly" to accurately localize it. Whether the owl determines target range before attacking or senses its approach toward the ground along a path of target interception is not known; extant data neither support nor reject either hypothesis (Refs. 79,125).

Synthetic sonars are probably capable of achieving localization accuracies as good as, and perhaps better than, the bats'. However, the relative time required to do so may significantly exceed that required by these animals. Accordingly, further work in this area would appear to be potentially rewarding for sonar technology. The owl's apparent ability to ascertain target range passively is truly exciting, and support of further (and expanded) study of this animal is urged.

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*There are minimal data available (Ref. 126) and the validity of some of these data has been questioned (Ref. 79). Also, measurements to date have employed pure tone stimuli. Natural stimuli for owls are probably broadband rustling, crunching, or chewing noises. Measurements performed with these kinds of stimuli would exhibit differences from the pure tone results.

V. PASSIVE/ACTIVE SONAR UTILIZATION

Some species of bats apparently exploit target radiated noise for early detection and localization of prey (Ref. 62). This is not a species' specific capability, but seems related only to bat/prey size. Absolute hearing sensitivity appears the same for all bats (and, indeed, is equivalent to other mammals). Accordingly, passive sonar capabilities of different species should be comparable in this regard. Large insect prey do radiate sound at intensities adequate to be exploited passively. On the other hand, small insect prey, e.g., fruit flies and mosquitoes, radiate sound at levels too low to be useful at any seemingly reasonable range to effect pursuit action (Ref. 51). The larger species of bats pursue and capture larger insect prey, while the smaller species pursue small insect prey. Therefore, it is likely the larger species rely on target radiated sounds for early detection and localization (there is some experimental evidence supporting this conjecture (Ref. 82)), while it is moot to know to what extent the smaller species do, if they do at all.

Confounding measurement on bats is the phenomenon of spatial or proprioceptive learning observed in the laboratory, but probably occurring to some degree in the wild. Given time to examine and learn their environment acoustically, bats reduce their echolocation (orientation) activity to a minimum and rely heavily upon apparent apperception of their own movements through it (Refs. 1,2,80,93, 104,105). It appears that they may not even attend to the few signals emitted during this activity (Refs. 3,44,80). They may be relying upon passive detection of environmental noises, e.g., the rustling of leaves, or, in the laboratory, detection of reflections of flight generated sounds or of noise generated by scraping or tapping their claws

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when crawling along a surface. That is, the bats may be exploiting a passive sonar capability for orientation (navigation) in familiar surroundings.

The owl's reliance upon and ability to use target radiated sounds has been discussed in preceding sections.

It is probable that whales rely (perhaps heavily) on passive detection and localization of prey or other sound radiating objects (e.g., ships), although this hypothesis is a difficult one to test. Available evidence is mostly anecdotal in nature. The killer whale, Orcinus orca, has not been detected echolocating in the wild and must be taught to use its capability in captivity (Ref. 37). The bottle-nose dolphin, T. truncatus, has been observed tracking live fish in its tank passively, and echolocated only when the ambient noise level was raised (the water filtration system was activated) (Refs. 10,37). Accordingly, it can be argued that many animals swimming together in a large herd would generate so much self-noise as to render passive target detection unlikely.

However, observation of a large group of dolphins feeding on a school of fish in relatively turbid water (limit of visibility ~50 cm) led to the conclusion that the dolphins were using only visual and passive acoustic clues to detect and capture individual prey (Ref. 25).

Finally, it has been observed that the dolphin in familiar surroundings performing a routine echolocation task becomes acoustically lazy, emitting apparently only a minimal number of signals requisite for the task, and these at very low intensities (Ref. 10). (A similar phenomenon of habituation to the task has also been observed in bats (Ref. 161).).

VI. CONCLUSIONS

The preceding overview of biological sonar phenomena is an attempt to place the knowledge of, and potential for, research in this area into perspective from the viewpoint of synthetic sonar technology. The guiding philosophy for this survey was to ascertain and illuminate those areas or activities of biological sonar research which might immediately or eventually influence, alter, or improve synthetic sonar development or design philosophy. This report is brief and, hopefully, to the point. The List of References is comprehensive, but represents only a portion of the literature surveyed. Much of the literature surveyed contributed to an understanding and appreciation of the problems, results, and direction(s) of research on biological sonar systems but was intrinsically of no significance with regard to bionics exploitation.

There is a message evident in bionics research on animal sonars. That is, the ear-brain is, without question, the best available adaptive processor for analyzing acoustic signals. Sonar technology has, for many valid reasons, sought to remove the ear-brain (the listener/operator) from the decision functions (detection/classification) of sonar operation. A baseline of sonar performance utilizing a motivated operator as an <u>acoustic</u> analyzer has never been established. A survey of biological sonars thus begs the recommendation that the utility of the sonar operator be reevaluated and that baseline sonar performance be established using the ear-brain processor.

Five areas of animal sonar research were recommended for continued or additional support because of their apparent potential to provide bionically useful information. Perhaps of most immediate consequence is study of the ability of the owl to localize and apparently range passively. Investigation of this phenomenon is proceeding with but minimal funding.* Accordingly, it is recommended that this work receive expanded support.

The second area has been a topic of investigation for many years with varying degrees of activity and with little or no success, primarily due to procedural reasons but often due to instrumentational shortcomings. This is the area of signal design for target classification: how are the interrogating signals modified to apparently optimize some target-specific characteristic of the echo? A methodological change was recommended. Given this change, research on both whales and bats appears ready to provide the required data, the work on whales through direct acoustic measurements, that on bats through electrophysiological techniques. Knowledge of the target acoustics is, of course, implicit.

Electrophysiological measurements are a direct approach in attempting to comprehend ear-brain functioning in the analysis of acoustic signals. The potential contribution of work in this area is great, but admittedly long-range. Support in this area, to the extent of maintaining an awareness of activities and results, was recommended. Understanding the animals' ability to localize a target in three-dimensional space is corollary to this work. More is known about bats in this area. Directivity of the external ear structures is a complex function of frequency, apparently permitting unique localization of a target in space with each echo. Knowledge of how bats achieve this localization might be exploited to facilitate analogous measurements by synthetic sonars. Therefore, it was recommended that work in this area be supported, at least to the extent of maintaining an awareness of activities and results.

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*The only known research being conducted in this country at this time is by Professor Mark Konishi, Department of Biology, Princeton University, under an NSF grant.

Finally, evolutionary evidence implies the delphinid sonar is optimal for underwater short range, high resolution applications. A bio-analog (electromechanical) simulation has been developed and is being used to examine the potential and limitations of the delphinid signal form (see Fig. 1). However, mechanical generation is inefficient and severely limits versatility. Accordingly, it was recommended that study of the dolphin's signal generator be supported, principally to guide development of possible new means of generating the high intensity, broadband signals required for exploitation of this sonar form, but also as the generator determines the limits of the animal's signal design capabilities.

Appendix II is a tabulation of available sonar and performance data for bats. One hundred three (103) genera and/or species are listed; Table A includes the Old World (Eastern hemisphere) bats; Table B, the New World (Western hemisphere) bats. Entries are alphabetical within each table. There are no obvious consistencies (or inconsistencies, for that matter) or trends evident in these data. What is obvious is that there is a multiplicity of signal forms used to solve many similar and diverse problems, all obviously successfully. What is also apparent is that in many areas there is a dearth of data extant.

Appendix III is a tabulation of available sonar and performance data for whales, dolphins, and porpoises. Nineteen (19) species are listed. Entries are alphabetical; there is no further breakdown. It is immediately apparent from this tabulation that there are appreciably fewer data available for these animals than for bats. The general trend apparent in these data is an inverse correlation between signal frequency (or absolute bandwidth) and physical size of the animal. All species seem to utilize a transient or very short pulse for echolocation.

Bibliographies of the accumulated literature for bats, whales, and other animals are included as Appendices IV, V, and VI, respectively. Entries are alphabetical by (senior) author, and chronological within an author's listing(s). Each entry has been coded using a 6-digit number. The coding key is shown at the beginning of each bibliography.

An annotated bibliography of selected papers, plus a compendium of selected translations of the foreign language literature, will be issued at a later date.

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APPENDIX I

BIOSONAR MEMBERSHIP CONTACTED

APPENDIX I

Biosonar Membership Contacted

Professor K. S. Norris, The University of California at Los Angeles. Professor Norris is presently attempting to establish a facility for Cetacean research, including echolocation, at The University of California Santa Cruz campus.

Professor A. D. Grinnell, The University of California at Los Angeles. Professor Grinnell has been active in electrophysiological investigations of neural correlates of echolocation phenomena in bats. One of his students, Miss Pat Brown, is examining the acoustic signals employed by bats for communication.

Professor A. Novick, Dr. O'D. W. Henson, Dr. George Pollak, Yale University. Professor Novick is completing a chapter on echolocation by bats to appear in Vol. 3 of The Biology of Bats, W. A. Wimsatt (ed.). Drs. Henson and Pollak are using chronic implants of electrodes to measure electrophysiological correlates of echolocation in free-flying bats.

Professor M. Konishi, Princeton University. Professor Konishi is measuring the ability of owls to localize and range upon target radiated noises, under various experimental conditions. He is the only person in the United States known to be studying target localization by owls. From the viewpoint of sonar technology, his results to date appear especially significant.

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Dr. James G. McCormick, Bowman-Gray School of Medicine, Wake-Forest University. Dr. McCormick is a pioneer in electrophysiological measurements of hearing phenomena in dolphins. He is presently examining the effects of hyperbarism on hearing in mammals.

Professor J. A. Simmons, Washington University. Professor Simmons is using artificial echoes to measure abilities of bats to resolve target range differences and to compensate for Doppler shifts caused by target and/or platform motion. He is attempting to instrument a fast response computer system to replay artificial echoes to echolocating bats at a programmed S/N value to examine the bat's ability to overcome jamming and the signal and/or noise parameters most affecting it. He is presently studying the ability of bats to resolve target aspect. A post-doctoral student, Dr. Glenis Long, working in Griffin's laboratory at The Rockefeller University, but primarily under Simmons' guidance, is measuring the ability of bats to resolve spectral differences in artificial echoes.

Professor N. Suga, Washington University. Professor Suga has been and continues to be active in electrophysiological measurements of both sound projecting and receiving phenomena in bats. He has recently demonstrated the existence of neural attenuation in the auditory brain during sound transmission, analogous to blanking in synthetic sonars, and has been able to electrically stimulate the bat brain to cause sound generation, a phenomenon being exploited to examine Doppler compensation by the CF bats.

Professor D. R. Griffin, The Rockefeller University. Professor Griffin is not presently actively involved in echolocation research. He is providing guidance for two post-doctoral students working in his laboratory: Dr. Glenis Long, mentioned above with Simmons, and Dr. Peter Hollander, who is attempting to measure the space-frequency characteristics of the bat's sound field. A third post-doctoral student, Dr. E. R. Buckler, from the University of Montana, will be in Professor Griffin's laboratory during the 1972-1973 academic year to study insect catching behavior of bats.

Dr. R. G. Busnel, Director, Laboratory of Physiological Acoustics, Jouy-en-Josas, France, and American Museum of Natural History. The French laboratory does research on all aspects of animal sound generation, reception, and correlated behavior, only a small part of which is related to classical echolocation. They were quite active at one time in recording and analysis of dolphin echolocation signals and behavior, but their efforts have been severely curtailed recently by lack of funds. The team they have applied to the problem consists of: Dr. J. C. Levy, Mathematician, currently developing a model for echolocation; Dr. A. Dziedzic, Engineer, responsible for the development and implementation of instrumentation; Dr. B. Escudie, Engineer, a student of Mermoz, and an enthusiastic advocate of correlational processing; and Dr. Busnel, Biologist. The team appears well-rounded and quite capable, but for reasons stated, has drifted out of the mainstream of echolocation research on dolphins. Dr. Levy is at the Jouy laboratory. Drs. Escudie and Dziedzic are at the Institute de Chemie et Physique Industrielle, Lyon. Dr. Escudie is presently working closely with Professor Simmons in analyses of bat signals.

Professor R. A. Suthers, Indiana University. Professor Suthers' interests have, in recent years, turned to problems of determining visual capabilities and usage in bats. He has begun investigation of the interaction between vision and echolocation as manifested by electrophysiological measurements performed in the inferior colliculus of the brain. Professor Suthers has one graduate student (name and academic level unknown) measuring the minimum audible angle (MAA) discrimination ability of bats. Professor Suthers, with Professor Suga, is writing a review of bat echolocation to appear in book form (Academic Press) late this year or early next year.

Dr. Donna J. Howell, Auditory Research Laboratories, Princeton University. Dr. Howell is beginning a post-doctoral fellowship at ARL (Princeton), continuing Simmons' work on target ranging by bats.

Miss Donna McDonald, University of Hawaii. Miss McDonald is attempting to measure MAA discriminability of the bottlenose dolphin. Her work is being performed at the NUC/Hawaii facility under supervision of Dr. W. W. L. Au.

Dr. E. C. Evans, III, Dr. W. W. L. Au, Mr. B. A. Powell, Mr. R. H. Penner, Mr. E. A. Murchison, NUC/Hawaii Laboratory.

Dr. C. S. Johnson, Mr. W. E. Evans, NUC/San Diego, California.

Foreign Membership Contacted:

Professor J. D. Pye, Kings College, University of London. Professor Pye for the past few years has been endeavoring to record and catalog the echolocation sounds of as many different species of bats as possible in the wild. To date, he has catalogued some 100 species. He has a doctoral student, L. H. Roberts, investigating the mechanics of signal generation and control by bats.

Dr. H. U. Schnitzler and Professor G. Neuweiler, University of Tubingen, Germany (at University of Frankfurt, beginning 1 January 1973). The efforts of this group are directed toward a behavioral and electrophysiological understanding of echolocation by the bat Rhinolophus ferrum-equinum. Immediately, an attempt will be made to explain the neurophysiological mechanism of Doppler compensation by this species of bat. Two students of Dr. Schnitzler's, E. Flieger and G. Schuller, are examining the echolocation abilities of this species of bat, and its apparent use of selected portions of its signal for location and ranging.

Professor S. Andersen, Odense University, Denmark. Professor Andersen has made both behavioral and acoustic measurements of echolocation by the harbor porpoise, Phocoena phocoena. He maintains one of the few members of this species in captivity. He has no plans to carry out any behavioral measurements of echolocation in the immediate future, but has done and will continue doing recording and analysis of the sounds emitted by this animal. Professor Andersen has two graduate students from Sweden who intend to examine the signals used by this species for communication. The latter work is contingent upon obtaining a second member of the species.

APPENDIX II

TABULATION OF BIOLOGICAL SONAR DATA FOR BATS

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TABLE A

TABULATIONS OF BIOLOGICAL SONAR DATA FOR OLD WORLD BATS

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I

SIGNAL CHARACTERISTICS

SPECIES	SIGNAL FORM	CONTINUOUS FREQUENCY: FREQUENCY, kHz	CONTINUOUS FREQUENCY: $\lambda^{(a)}$, mm	CONTINUOUS FREQUENCY: DURATION, msec	CONTINUOUS FREQUENCY: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	FM: FREQUENCY SWEEP, kHz	FM: $\Delta\lambda^{(a)}$, mm	FM: DURATION, msec	FM: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	REMARKS	REFERENCES
Asellia tridens	CF/FM	115-120 120 117	~3 2.9 2.9	6.8 ~9		120-95 120-60 117-95	3-3.6 2.9-5.8 2.9-3.6	~1		Major component - 2nd harmonic; pulses produced in groups--groups of 1-10 within 170 msec; instantaneous repetition rates up to 75 pulses/sec	Pye and Roberts 1970 Moehres and Kulzer 1955 Roberts 1972
Aselliscus tricuspidatus	Mixed	112	3.1	1.6-2.4		112-94	3.1-3.7	1.1		Tropical	Grinnell 1972
Emballonura nigrescens	Mixed FM	61 (2nd harmonic)	5.6	0-0.25		61-37 (2nd harmonic)	5.6-9.3	0.6-1.3		Multiple harmonics Tropical	Grinnell 1972
Eptesicus tenuipinnis	FM					62-37	5.5-9.3	0.9-1.9	110	Temperate	Novick 1958
Hipposideros beatus maximus	CF	100-114	3.4-3	~8	~95					Hand held Tropical	Novick 1958
Hipposideros brachyotus	CF	85-93	4-3.7	5-8						Hand held Tropical	Novick 1958
Hipposideros caffer	CF/FM	140-150 137	2.5-2.3 2.5	6-23		 137-100	 2.5-3.4			Tropical	Pye and Roberts 1970 Roberts 1972

(a) C = 344mm/msec

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I
SIGNAL CHARACTERISTICS

SPECIES	SIGNAL FORM	CONTINUOUS FREQUENCY: FREQUENCY, kHz	CONTINUOUS FREQUENCY: $\lambda^{(a)}$, mm	CONTINUOUS FREQUENCY: DURATION, msec	CONTINUOUS FREQUENCY: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	FM: FREQUENCY SWEEP, kHz	FM: $\Delta\lambda^{(a)}$, mm	FM: DURATION, msec	FM: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	REMARKS	REFERENCES
Hipposideros calcaratus	mixed	62	5.5			62-50	5.5-6.9			No clear evidence that Hipposideros more skillful at echolocation than any other Hipposideros Hipposideros - general correlation between size of bat and frequency used Frequency pattern - principal frequency one octave higher than a very low amplitude component Primarily 2nd harmonic Tropical	Grinnell 1972 Roberts 1972
		128 (2nd harmonic)	2.7	3.4-4.6		128-97 (2nd harmonic)	2.7-3.5	~1			
Hipposideros commersoni	CF/FM	56-68 56 and 66	6.1-5 6.1 and 5.2	9-20		66-57	5.2-6.9	3-3.5		Possibly subspecies differentiation; frequency correlated with body size	Pye and Roberts 1970 Pye 1972 Roberts 1972
Hipposideros cupidus	mixed	123	2.8	2.2-2.8		123-97	2.8-3.5	0.8			Grinnell 1972 Roberts 1972
Hipposideros cyclops	CF	101-109	34-32	17-24	~115					Hand held Tropical	Novick 1958
Hipposideros diadema	mixed CF	58 (2nd harmonic)	5.9	4.8-9.1		58-47 (2nd harmonic)	5.9-7.3	~1		Four harmonics detectable in Hipposideros diadema Tropical	Grinnell 1972 Roberts 1972
Hipposideros galeritus		145	2.4	1.9-3.6		145-120	2.4-2.9	~1		Tropical	Grinnell 1972 Roberts 1972

(a) C = 344mm/msec

I

SIGNAL CHARACTERISTICS

SPECIES	SIGNAL FORM	CONTINUOUS FREQUENCY				FM				REMARKS	REFERENCES
		FREQUENCY, kHz	$\lambda^{(a)}$, mm	DURATION, msec	SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	FREQUENCY SWEEP, kHz	$\Delta\lambda^{(a)}$, mm	DURATION, msec	SPL, dB re 0.0002 $\frac{dyne}{cm^2}$		
Hipposideros lankandiva	CF	57-74	6-4.6	8-13	~130	Down, 2-8 (55-67)	0.3-0.5			Hand held Tropical	Novick 1958
Hipposideros obscurus	CF	95-109	3.6-3.3	9	~125					Hand held Tropical	Novick 1958
Hipposideros s. speoris	CF	80-120	4.3-2.9	6-10	120-135					Hand held Tropical	Novick 1958
Miniopterus australis paulus	FM					50-17	6.9-20	1.1-2.8		Hand held; 2nd and 3rd harmonics	Novick 1958
Miniopterus fuliginosus	FM					~55-35	6.3-9.8	1.9-3.3	115-120	Hand held	Novick 1958
Miniopterur natalensis	FM					82-50	4.2-6.9	2.7-3.6		Hand held	Novick 1958
Miniopterus schreibersii eschscholtzii	FM					87-40	4-8.6	1.5-3.7	~138	Tropical	Novick 1958
Miniopterus tristis	FM					46-30	7.5-11.5	2.9-6.5	~135	Hand held	Novick 1958

(a) C = 344mm/msec

I

SIGNAL CHARACTERISTICS

SPECIES	SIGNAL FORM	CONTINUOUS FREQUENCY: FREQUENCY, kHz	CONTINUOUS FREQUENCY: $\lambda^{(a)}$, mm	CONTINUOUS FREQUENCY: DURATION, msec	CONTINUOUS FREQUENCY: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	FM: FREQUENCY SWEEP, kHz	FM: $\Delta\lambda^{(a)}$, mm	FM: DURATION, msec	FM: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	REMARKS	REFERENCES
Lyraderma l. lyra	CF	60-80	5.7-4.3		100-105					Tropical	Novick 1958
Megaderma lyra	CF	58.5 (3rd harmonic) 78.5 (4th harmonic)	5.9 4 4	1.2 (0.4-1.8)						Multiple harmonics Pulses extremely short; varies 1300 μsec related to orientational situation. Longer signals are produced in free and unimpeded flight in open space. Shorter (less than 1000 μsec) and higher frequency sounds are produced by nonflying bats exploring environment, or flying bats in approaching a goal or obstacle. Highest frequency - most intense Frequency modulation is nearly absent Tropical	Novick 1962 Schnitzler 1967 Mohres 1967
Megaderma s spasma	CF	20	17.2							2nd and 3rd harmonics present from beginning at significant amplitudes while 4th harmonic sometimes appeared late in pulse Tropical	Novick 1958

(a) C = 344mm/msec

I

SIGNAL CHARACTERISTICS

SPECIES	SIGNAL FORM	CONTINUOUS FREQUENCY: FREQUENCY, kHz	CONTINUOUS FREQUENCY: $\lambda^{(a)}$, mm	CONTINUOUS FREQUENCY: DURATION, msec	CONTINUOUS FREQUENCY: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	FM: FREQUENCY SWEEP, kHz	FM: $\Delta\lambda^{(a)}$, mm	FM: DURATION, msec	FM: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	REMARKS	REFERENCES
Myotis macrotarsus	FM					50-27	6.9-12.7	2.3-3.7	130	Temperate	Novick 1958
Myotis myotis	FM					75-30 (search)	4.6-11.5	1.5-1.0		Temperate	Simkin 1969
						45-25 (terminal)	7.6-13.8	0.5-0.3			
Myotis oxygnathus	FM					105-30 (search)	3.3-11.5	3.5-1.5		Temperate	Simkin 1970
						60-30 (terminal)	5.7-11.5	1.5-0.5			Konstantinov and Akhmarova 1968
											Simkin 1969
											Airapetiantz and Konstantinov 1967
											Airapetiantz, Konstantinov, and Matjushkin 1969
											Konstantinov 1969
Nycteris arge	CF	20-22 (1st harmonic)	17-15	0.4-1.4	110-120					3-5 Harmonics Hand held Tropical	Novick 1958
Nycter.s grandis	CF	20-22 (1st harmonic)	17-15	0.4-1.4	110-120					3-5 Harmonics Hand held Tropical	Novick 1958
Nycteris hispida	CF	20-22 (1st harmonic)	17-15	0.4-1.4	110-120					3-5 Harmonics Hand held Tropical	Novick 1958

(a) C = 344mm/msec

I

SIGNAL CHARACTERISTICS

SPECIES	SIGNAL FORM	CONTINUOUS FREQUENCY				FM				REMARKS	REFERENCES
		FREQUENCY, kHz	$\lambda^{(a)}$, mm	DURATION, msec	SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	FREQUENCY SWEEP, kHz	$\Delta\lambda^{(a)}$, mm	DURATION, msec	SPL, dB re 0.0002 $\frac{dyne}{cm^2}$		
Pipistrellus c. ceylonicus	FM					35-25	9.8-13.8	1.7-3.3	95-105*	*At 15 cm from head Tropical	Novick 1958
Pipistrellus coramandra	FM					71-28	4.8-12.3	0.8-3.6	110-115	Hand held	Novick 1958
Pipistrellus m. mimus	FM					60-37	5.7-9.3	2.2-4.3		Hand held	Novick 1958
Pipistrellus papuanus	FM					75-35	4.6-10	1-2			Grinnell 1972
Rhinolophus alcyone	CF/FM	85-90 89	4-3.8 3.9	11-60		89-69	3.9-5				Pye and Roberts 1970 Roberts 1972
Rhinolophus a. arcuatus	CF/FM	55-65	6.3-5.3	17-34		~66-51	5.2-6.8			Hand held	Novick 1958
Rhinolophus euryale	CF/FM	103-104	3.3	35-45 (search) 7-10 (burst)		103-90	3.3-3.8	1.5-3		Flying animals lower the frequency of the CF part by such an amount that the Doppler shifts caused by flight velocity are compensated. Use burst pulse transmission mode during terminal phase of pursuit or landing	Schnitzler 1967 Pye and Roberts 1970

(a) C = 344mm/msec

I

SIGNAL CHARACTERISTICS

SPECIES	SIGNAL FORM	CONTINUOUS FREQUENCY: FREQUENCY, kHz	CONTINUOUS FREQUENCY: $\lambda^{(a)}$, mm	CONTINUOUS FREQUENCY: DURATION, msec	CONTINUOUS FREQUENCY: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	FM: FREQUENCY SWEEP, kHz	FM: $\Delta\lambda^{(a)}$, mm	FM: DURATION, msec	FM: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	REMARKS	REFERENCES
Rhinolophus ferrum equinum	CF/FM	83.3 (at rest)	4.1	up to 100, 25-50 average (search) 10, burst mode burst duration 30-60	105-135	83-56	4.1-6.1	~1.5	+6-10 dB re CF during pursuit/avoidance	Very intense 2nd harmonic of weak fundamental frequency of 41.5 kHz Flying bats lower frequency of CF part to compensate for Doppler shifts due to target or bat motion. Frequency varies between 81.0 and 83.3 kHz dependent on flight velocity, whereas echo frequency is kept constant at 83.3 kHz Uses burst pulse mode of 2 to 10 short pulses/burst during insect capture or obstacle avoidance With decreasing sound duration, duration of FM part diminishes. CF portion continually sacrificed for FM portion, but never completely disappears	Airapetianz, Konstantinov, and Matjushkin 1969 Konstantinov and Sokolov 1969 Novick 1971 Neuweiler, Schuller, Schnitzler 1971 Schnitzler 1967 Neuweiler 1970 Schnitzler 1970 Webster 1963 Simmons 1969, 1971, 1972 Mogus 1967 Pye 1960, 1961 Griffin, Dunning, Cahlander, Webster 1962 Griffin 1962 Novick 1958 A. Pye 1967

(a) C = 344mm/msec

I
SIGNAL CHARACTERISTICS

SPECIES	SIGNAL FORM	CONTINUOUS FREQUENCY: FREQUENCY, kHz	CONTINUOUS FREQUENCY: $\lambda^{(a)}$, mm	CONTINUOUS FREQUENCY: DURATION, msec	CONTINUOUS FREQUENCY: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	FM: FREQUENCY SWEEP, kHz	FM: $\Delta\lambda^{(a)}$, mm	FM: DURATION, msec	FM: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	REMARKS	REFERENCES
Rhinolophus fumigatus	CF/FM	45-50	7.7-6.9		15-65						Pye and Roberts 1970
		45	7.7			45-33	7.7-10.5				Roberts 1972
Rhinolophus hipposideros	CF/FM	105-115	3.3-3	15-65							Pye and Roberts 1970
		109	5.2			109-80	5.2-4.3				Roberts 1972
Rhinolophus landeri	CF/FM	115-122	3-2.8	14-72							Pye and Roberts 1970
		121	2.8			121-80	2.8-3.4				
Rhinolophus luctus	CF	42	8.2	42-30	8.2-11.5						Roberts 1972
Rhinolophus mehelyi	CF/FM	105	3.3	~35	3.3-3.8	105-90	1.5-3			During pursuit/avoidance uses burst pulse transmission; up to 8 pulses/burst; bursts correlated with respiration	Konstantinov and Sokolov 1969
Rhinolophus r. rouxi	CF	60-75	5.7-4.6	21-45	~130	~65-60	5.3-5.7			Hand held	Novick 1958
Rhinolophus s. rubrufus	CF/FM	45 (2nd harmonic)		26-42 with extremes of 15-60 msec	134	82-51	4.2-6.7				Novick 1958
		62-82 (dominant)	5.5-4.2								
Rousettus sp. (Megachiroptera)										Generates clicks by movements of the tongue and emits these through corner of mouth Principal frequencies, 12 and 18 kHz, depending on species and individual; overtones and harmonics present to a considerable degree Tropical	Griffin, Novick, Kornfield 1958

(a) C = 344mm/msec

I
SIGNAL CHARACTERISTICS

SPECIES	SIGNAL FORM	CONTINUOUS FREQUENCY				FM				REMARKS	REFERENCES
		FREQUENCY, kHz	λ(a), mm	DURATION, msec	SPL, dB re 0.0002 dyne/cm²	FREQUENCY SWEEP, kHz	Δλ(a), mm	DURATION, msec	SPL, dB re 0.0002 dyne/cm²		
Tadarida luzonus	FM					43-25	8-13.8	6.3-10			Novick 1958
Tadarida midas	FM					22-11	15.5-31	7-10		Hand held	Novick 1958
Tadarida tragata	FM					28-12.5	12.3-27.5	3.1-8.1	110-115		Novick 1958
Taphazous melanopogon	FM					15-12	22.9-28.7	5.1		Fundamental, with 2nd, 3rd, 4th harmonics Tropical	Novick 1958
Taphozous philip .nensis	FM					16-13	21.5-26.5	4.6		Fundamental, plus 2nd-4th harmonics Tropical	Novick 1958
Triaenops afer	CF/FM	78-92 79 and 88	4.4-3.7 4.4 and 3.9	6-16		~85-65	4-5.3	~3		Bimodality evident only in groups Tropical	Fye and Roberts 1970 Fye 1972 Roberts 1972
Tylonycteris pachypus meyeri	FM					80-53	4.3-6.5	1.5-5	130-145	Tropical	Novick 1958
Vespertilio kuhlii	FM					80-35	4.3-9.8	1-2.2		Orientation signals short (1-3 msec); signals longer flying in open space far from obstacles; longer in species which fly at high velocity and hunt in open areas. Temperate	Simkin 1970

(a) C = 344mm/msec

I
SIGNAL CHARACTERISTICS

SPECIES	SIGNAL FORM	CONTINUOUS FREQUENCY: FREQUENCY, kHz	CONTINUOUS FREQUENCY: $\lambda^{(a)}$, mm	CONTINUOUS FREQUENCY: DURATION, msec	CONTINUOUS FREQUENCY: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	FM: FREQUENCY SWEEP, kHz	FM: $\Delta\lambda^{(a)}$, mm	FM: DURATION, msec	FM: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	REMARKS	REFERENCES
Vespertilio murinus	FM					50-20	6.9-17.2	0.6-1.6		Temperate	Simkin 1970
Vespertilio nathusii	FM					90-30	3.8-11.4	0.8-2.9		Temperate	Simkin 1970
Vespertilio nilssonii	FM					50-22	6.9-15.6	2-3		Temperate	Simkin 1970
Vespertilio ognevi	FM					75-25	4.6-13.8	1.5		Temperate	Simkin 1970
Vespertilio savii	FM					80-30	4.3-11.5	0.7-2.0		Temperate	Simkin 1970
Vespertilio serotinus	FM					60-30	5.7-11.4	1.4-2.2		Has 2nd and sometimes 3rd harmonic component Temperate	Simkin 1970
Vespertilio superans	FM					50-19	6.9-18.1	1.2-4.5		Temperate	Simkin 1970

(a) C = 344mm/msec

II
SONAR CHARACTERISTICS

SPECIES	FLYING SPEED, m/sec	PRR, sec⁻¹	CONTINUOUS FREQUENCY: BEAMWIDTH, deg	FM: Δ BEAMWIDTH, deg	FM: RANGE RESOLUTION, mm Δt	FM: RANGE RESOLUTION, mm Δf	REMARKS	REFERENCES
Megaderma lyra	(see remarks)	10-50 (average) to 300 (peak)	70 (-3 dB) 60 (-3 dB)				When approaching an obstacle, emits pulses in doublets Can hover in flight Assumed dipole source (double emitter, nostrils separated by λ/2)	Mogus 1970 Mohres 1967 Novick 1958
Myotis myotis		15-30 40-60 (burst) to 200 (terminal)			~26 ~4 (terminal)	~ 0.3 ~5	Pulses emitted in packets, or volleys, of 2 to 6 pulses/packet during approach to target	Simkin 1969
Myotis oxygnathus		7-10 (search) 40-60 (burst) 100 (terminal)			25-70 (search) 8-17 (terminal)	~0.25 ~0.8	Pulses emitted in packets, or volleys, of 2 to 6 pulses/packet during approach to target	Simkin 1970, 1969 Airapetianz, Konstantinov, and Matjushkin 1969
Rhinolophus ferrum equinum	4-5	5-20 (search) 70-80 (burst) 4-8 (burst rate)	60 (-3 dB) (calculated) (horizontal) 52 (-3 dB) (horizontal) 20 (-1.5 dB) 70 (-3 dB) vertical		~260	~10	When investigating unknown object, it emits bursts of shorter pulses, up to 20/burst, at increased pulse repetition frequency, e.g., average PRR during volley of 8 pulses is 35/sec. Pulse duration during burst is ~10 msec. Assumed dipole source (double emitter; nostrils separated by λ/2) Apparent dipole source, both planes	Airapetianz, Konstantinov, and Matjushkin 1969 Konstantinov and Sokolov 1969 Schnitzler 1970, 1967 Mogus 1970, 1967 Pye 1960 Griffin, Dunning, Cahlander, Webster 1962 Novick 1961 Sokolov and Makarov 1971

III
AUDIOMETRIC DATA

SPECIES	AUDIOGRAM[a]	FREQUENCY RANGE, kHz	MAXIMUM SENSITIVITY FREQUENCY, kHz	MAXIMUM SENSITIVITY SPL, dB re 0.0002 dyne/cm²	REMARKS	REFERENCES
Aselliscus tricuspidatus	Electrophysiological (N_4)	10-150	50 90-110	25	Roll-offs 10-100 dB/0.01 Δf; single units (neurons), 500-1500 dB/octave	Grinnell 1972
Emballonura nigrescens	Electrophysiological (N_4)	10-120	50-65	25		Grinnell 1972
Hipposideros calcaratus	Electrophysiological (N_4)	10-140	50-60 100-130	30		Grinnell 1972
Hipposideros diadema	Electrophysiological (N_4)	10-90	50-60	30		Grinnell 1972
Hipposideros galeritus	Electrophysiological (N_4)	10-150	60-70 120-140	30-35		Grinnell 1972
Myotis oxynathus	Behavioral; operant conditioning	0.5-250	40 (10-90)	-13 (40 kHz)	Bats continued to react to all frequencies presented up to limits of generator used--frequency of 250 kHz displaying level of positive responses higher than 70%	Konstantinov, Sanotskaya, and Sokolova 1971 Airapetians and Konstantinov 1971
Pipistrellus papuanus	Electrophysiological (N_4)	10-110	40-90	40		Grinnell 1972

[a]BEHAVIORAL; TASK
ELECTROPHYSIOLOGICAL

III
AUDIOMETRIC DATA

SPECIES	AUDIOGRAM[c]	FREQUENCY RANGE, kHz	MAXIMUM SENSITIVITY FREQUENCY, kHz	MAXIMUM SENSITIVITY SPL, dB re 0.0002 dyne/cm^2	REMARKS	REFERENCES
Rhinolophus euryale	Electrophysi-ological (N_4)	<50-130	50-95 104	25-40 ~10		Schnitzler, Schuller, and Neuweiler 1971
Rhinolophus ferrum equinum	Electrophysi-ological (N_4)	10-100	20-40 and 83.3	0-5	Threshold increases by an average of 6.5 dB/0.1% Δf when signal frequency is lowered by 100 Hz Average threshold slope of 40-55 dB/1.8 kHz	Airapetianz, Konstantinov, and Matjushkin 1969 Vasil'ev 1967 Neuweiler 1970 Neuweiler, Schuller, Schnitzler 1971
Rousettus amplexicaudatus stresemanii	Electrophysi-ological (N_4)	10-100	45-50	50	Roll-off of 20-30 dB/octave, $f < 45$ kHz; 125-150 dB/octave, $f > 50$ kHz	Grinnell and Hagiwara 1972

[c]BEHAVIORAL; TASK
ELECTROPHYSIOLOGICAL

IV
DETECTION/DISCRIMINATION DATA

SPECIES	TARGET/OBSTACLE; DETECTION/DISCRIMINATION					SIGNAL; DETECTION, DISCRIMINATION, LOCALIZATION				REMARKS	REFERENCES
	FORM/MATERIAL	SIZE, cm	TASK	DISTANCE, cm	PERFORMANCE	TECHNIQUE[a]	SIGNAL FORM	TASK	PERFORMANCE		
Hipposideros diadema						electro-physiological (N_4)	tone burst	recovery, time interval 50% 100%	3 msec 6-8 msec		Grinnell 1972
Hipposideros galeritus						electro-physiological (N_4)	tone burst	recovery, time interval 100%	2 msec		Grinnell 1972
Megaderma lyra	nylon monofilament, grid barrier (14 cm separation)	0.008 0.006	avoidance		>50% 18%						Mohres 1967
Myotis myotis	discs squares triangles 6-point stars, aluminum	equal area (disc, 5 diam)	discrimination, shape								Simkin 1969
Myotis oxynathus	discs squares triangles 6-point stars, aluminum	equal area (disc, 5 diam)	discrimination, shape								Simkin 1969
	multistage pyramid	base, 10x10	detection and recognition							Retraining to small pyramid, signal duration diminished 30%	Simkin 1970

[a] BEHAVIORAL; TASK ELECTROPHYSIOLOGICAL

IV
DETECTION/DISCRIMINATION DATA

SPECIES	TARGET/OBSTACLE; DETECTION/DISCRIMINATION: FORM/ MATERIAL	SIZE, cm	TASK	DISTANCE, cm	PERFORMANCE	SIGNAL; DETECTION, DISCRIMINATION, LOCALIZATION: TECHNIQUE[c]	SIGNAL FORM	TASK	PERFORMANCE	REMARKS	REFERENCES
Myotis oxynathus (Cont'd)	small multistage pyramid	base 4.4x4.4	detection and recognition, selection in presence of large pyramid and sphere								
	spheres	4.4 and 2.9	detection and recognition, selection in presence of pyramid and other spheres							Identification of spheres, uses long, high frequency signals	
	square versus triangle and disc	equal area (156 cm^2)	discrimination, shape	160-360	~90%					Approached positive shape alone. Did not approach negative shape alone	Konstantinov and Akhmarova 1968
	squares (6)	area, 156 cm^2 to 625 cm^2	discrimination, size	160-360	95%, 156 cm^2 versus 625 cm^2 80%, 156 cm^2 versus 172 cm^2						
	square, aluminum, versus square, plywood	area 156 cm^2	discrimination, material	160-360	87%						
	metal wire barrier	0.008	avoidance							Calculated echo level, -1.5 dB re 0.0002 $dyne/cm^2$	Airapetianz and Konstantinov 1971
	cylinders	20 long				behavioral		discrimination, target range difference R=1 m	75%, ΔR=2.5 cm (Δt:160 μsec)		

(c)BEHAVIORAL; TASK
ELECTROPHYSIOLOGICAL

IV
DETECTION/DISCRIMINATION DATA

SPECIES	TARGET/OBSTACLE; DETECTION/DISCRIMINATION: FORM/MATERIAL	SIZE, cm	TASK	DISTANCE, cm	PERFORMANCE	SIGNAL; DETECTION, DISCRIMINATION, LOCALIZATION: TECHNIQUE[c]	SIGNAL FORM	TASK	PERFORMANCE	REMARKS	REFERENCES
Myotis oxynathus (Cont'd)	squares, aluminum brass plexiglass	14x14	discrimination:								Airapetianz, Konstantinov, and Matjushkin 1969
			edge smooth versus serrated		70%-100%						
			contour plane versus convex		70%-100%						
			material metal versus metal		50%						
			metal versus other		70%-100%						
Nyctalus noctula	cube cylinder pyramid, plastic	equal volumes	discrimination, form	20-50							Airapetianz and Konstantinov 1965
Pipistrellus papuanus						electrophysiological (N_4)	tone burst	recovery, time interval 50% 100%	1-1.5 msec 2 msec		Grinnell 1972
Plecotus auritus	cube cylinder pyramid, plastic	equal volumes	discrimination, form	30-50							Airapetianz and Konstantinov 1965
Rhinolophus euryale	metal wire barrier (17.5 cm separation)	0.02 0.008	avoidance		70% 68%						Schnitzler 1967

(c) BEHAVIORAL; TASK ELECTROPHYSIOLOGICAL

IV
DETECTION/DISCRIMINATION DATA

SPECIES	TARGET/OBSTACLE; DETECTION/DISCRIMINATION					SIGNAL; DETECTION, DISCRIMINATION, LOCALIZATION				REMARKS	REFERENCES
	FORM/ MATERIAL	SIZE, cm	TASK	DISTANCE, cm	PERFORMANCE	TECHNIQUE[c]	SIGNAL FORM	TASK	PERFORMANCE		
Rhinolophus ferrum-equinum	cylinders	20 long				behavioral		discriminate target range difference; R=1 m	75%; ΔR=4 cm (Δt:250 μsec)		Airapet'anz and Konstantinov 1971
	cylinders	20 long				behavioral		discriminate crossrange target separation; R=2.5 m	4°30'		
	squares, aluminum brass plexiglass	14x14	discrimination: edge smooth versus serrated		70%-100%						Airapetianz, Konstantinov, and Matjushkin 1969
			contour plane versus convex		70%-100%						
			material metal versus metal		50%						
			metal versus other		70%-100% 70%-100%						
						behavioral, artificial echo	tone burst	compensate for simulated target velocity (Doppler)	ΔV:0.2 m/sec (~50 Hz @ 80 kHz)		Simmons 1972
	metal wire barrier (17.5 cm separation)	0.02 0.008	avoidance		70% 50%						Schnitzler 1967
	square	20x20	recognition	1000							Mohres 1960

[c] BEHAVIORAL; TASK
ELECTROPHYSIOLOGICAL

IV
DETECTION/DISCRIMINATION DATA

SPECIES	TARGET/OBSTACLE; DETECTION/DISCRIMINATION					SIGNAL; DETECTION, DISCRIMINATION, LOCALIZATION				REMARKS	REFERENCES
	FORM/ MATERIAL	SIZE, cm	TASK	DISTANCE, cm	PERFORMANCE	TECHNIQUE[c]	SIGNAL FORM	TASK	PERFORMANCE		
Rhinolophus mehelyi	metal wire barrier (50 cm separation)	0.008	avoidance		~75%-80%						Konstantinov, Sokolov, and Stosman 1967
Rousettus aegypticus (megachiroptera)	metal wire barrier (53 cm separation)	0.15 diam 0.107 diam	avoidance		77% 68%					Are more vulnerable to noise interference than Vespertilionidae	Griffin, Novick, and Kornfield 1958

[c] BEHAVIORAL; TASK ELECTROPHYSIOLOGICAL

V
HABITAT/PREY/BIOLOGY

SPECIES	SIZE	HABITAT	BEHAVIOR	PREY	REMARKS	REFERENCES
Asellia tridens		desert, palm groves, Old World	Fly swiftly near ground			Walker 1968
Hipposideros sp.		paleotropical	Flv close to ground. Hr insects in flight while following contours of ground and vegetation	insects (beetle, termites, cicadas) fruit		Novick 1958; Walker 1968
Megaderma sp.	20-50 g	Feed among trees and undergrowth. paleotropical	Adept flyers. Can hover in flight. Hunt along solid surfaces	sitting or crawling small insects and vertebrates; carnivorous	Heavily reliant upon vision under normal circumstances	Mohres 1967; Novick 1958; Walker 1968
Miniopterus sp.	8-20 g	tropical and temperate zones of Old World	Rapid, jerky flight. Feed at altitudes of 10-20 m	insects		Novick 1958; Walker 1968
Myotis macrotarsus				fish and insects		Novick 1958
Myotis oxygnathus	6-7.5 cm long		High maneuverability in flight	insects		Konstantinov and Akhmarova 1968
Nycteris sp.	to 30 g	rain forest to arid plains paleotropical	Hunt insects on solid surfaces	insects (moths, beetles)		Novick 1958; Walker 1968

Y
HABITAT/PREY/BIOLOGY

SPECIES	SIZE	HABITAT	BEHAVIOR	PREY	REMARKS	REFERENCES
Nyctalus noctula	15-40 g	tropical and temperate zones of Old World	High maneuverability in flight	small animals--rodents winged insects--beetles, ants, moths		Gould 1955 Walker 1968
Pipistrellus sp.	~4-8 g	worldwide	Jerky flight	insects (moths, mosquitoes, gnats)		Walker 1968
Plecotus auritus	5-20 g	temperate regions of Old World	Hover in flight. Hunt insects on solid surfaces	insects (moths, beetles)		Novick 1958 Gould 1955 Walker 1968
Rhinolophus sp.	to 28 g	Tropical and temperate zones of Old World. Prefer open country for hunting. Feed near and on ground	Flight may be swift, straight, and sometimes high	insects (moths, beetles, spiders)		Novick 1958 Schnitzler 1970 Walker 1968
Taphazous sp.	10-30 g	open areas paleotropical		insects		Novick 1958 Walker 1968
Tylonycteris pachypus	smallest known bat	paleotropical		insects		Novick 1958

V
HABITAT/PREY/BIOLOGY

SPECIES	SIZE	HABITAT	BEHAVIOR	PREY	REMARKS	REFERENCES
Vespertilio kuhlii*		open country	Fly near ground	insects and fish (mosquitoes)	*Walker lists only two species of the genus Vespertilio: V. murinus and V. superans, found in temperate regions of Old World	
Vespertilio murinus	14 g	forests and river valleys	Fly high above ground	insects and fish (mosquitoes, beetles, moths, butterflies)		
Vespertilio nathusii		temperate forest areas and water courses	Fly high above ground	insects and fish (mosquitoes)		Simkin 1970 Walker 1968
Vespertilio nilsonii		near forest areas		insects and fish (mosquitoes)		
Vespertilio ognevi				insects and fish		
Vespertilio savii		grassy plains, along water courses		insects and fish (mosquitoes)		
Vespertilio serotinus		open country, sand dunes	Fly near ground. Can hover in flight	insects and fish (beetles)		
Vespertilio superans				insects and fish (mosquitoes)		

TABLE B

TABULATIONS OF BIOLOGICAL SONAR DATA FOR NEW WORLD BATS

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I
SIGNAL CHARACTERISTICS

SPECIES	SIGNAL FORM	CONTINUOUS FREQUENCY: FREQUENCY, kHz	CONTINUOUS FREQUENCY: $\lambda^{(a)}$, mm	CONTINUOUS FREQUENCY: DURATION, msec	CONTINUOUS FREQUENCY: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	FM: FREQUENCY SWEEP, kHz	FM: $\Delta\lambda^{(a)}$, mm	FM: DURATION, msec	FM: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	REMARKS	REFERENCES
Anoura geoffroyi	FM					~100-50	3.4-6.9	~0.5-2		Tropical	A. Pye 1967
Artibeus cinereus	FM					90-60	3.8-5.7			Tropical	A. Pye 1967
Artibeus jamaicensis palmarum	FM					56-31 65-42	6.1-11.1 5.3-8.2	2.7-3.2 1-3	 95	Signal accompanied by strong 2nd harmonic	Novick 1963 Griffin and Novick 1955 A. Pye 1967
Artibeus lituratus	FM					65-40	5.1-8.6			Tropical	A. Pye 1967
Balantiopteryx plicata	FM					18-15	18.9-22.9		2-4.2	Multiple harmonics Tropical	Novick 1962
Carollia perspicillata	FM					80-55 (2nd harmonic)	4.3-6.3	0.5-1		Tropical	Griffin and Novick 1955 Grinnell 1970 A. Pye 1967
Centurio senex	FM					115-70	3-4.9	2		Tropical	A. Pye 1967
Chilonycteris personata mexicana	FM					53-38	6.5-9.1	~3.2		Tropical	Novick 1963 Griffin and Novick 1955

(a) C = 344mm/msec

I
SIGNAL CHARACTERISTICS

SPECIES	SIGNAL FORM	CONTINUOUS FREQUENCY				FM				REMARKS	REFERENCES
		FREQUENCY, kHz	$\lambda^{(a)}$, mm	DURATION, msec	SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	FREQUENCY SWEEP, kHz	$\Delta\lambda^{(a)}$, mm	DURATION, msec	SPL, dB re 0.0002 $\frac{dyne}{cm^2}$		
Chilonycteris psilotis	Mixed	~21 (1st harmonic)	16.4	3-5 (search) 0.6-1 (terminal)		21-17	16.4-20	~1		1st and 2nd harmonics always present Maintains constant pulse-echo overlap (~1 msec) during pursuit FM occurs midway in pulse Tropical	Novick 1965 Novick 1971
Chilonycteris rubiginosa (chilonycteris parnellii)	CF	32 (1st harmonic) 64 (2nd harmonic)	10.8 5.4	14-26 (search) 9 (terminal)		32-28 64-56	10.8-12.3 5.4-6.7	1.5-2		2nd harmonic dominant At rest--maintains frequency within ±100 Hz of average frequency In flight--lowers frequency to compensate for Doppler shifts caused by flight velocity. Appears to detect insects initially by pulse-echo overlap Following detection, pulse duration increases until pulse-echo overlap exceeds 17-18 msec. Uses burst pulse transmission mode during pursuit or landing; up to 30 pulses/burst; pulse duration: 4 msec Tropical	Novick 1971 Novick 1965 Novick and Vaisnys 1964 Grinnell 1970 Griffin and Novick 1955 Mogus 1967 A. Pye 1967 Schnitzler 1970
Chiroderma villosum	FM					102-60	3.4-5.7	1.0-1.5		Signal contains several harmonics Tropical	A. Pye 1967
Desmodus rotundus murinus	FM					75-48 (2nd harmonic)	4.6-7.2	0.8-1.6		2nd harmonic present at high amplitude Tropical	Novick 1965 A. Pye 1967 Griffin and Novick 1955

(a) C = 344mm/msec

I

SIGNAL CHARACTERISTICS

SPECIES	SIGNAL FORM	CONTINUOUS FREQUENCY: FREQUENCY, kHz	CONTINUOUS FREQUENCY: $\lambda^{(a)}$, mm	CONTINUOUS FREQUENCY: DURATION, msec	CONTINUOUS FREQUENCY: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	FM: FREQUENCY SWEEP, kHz	FM: $\Delta\lambda^{(a)}$, mm	FM: DURATION, msec	FM: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	REMARKS	REFERENCES
Eptesicus fuscus	FM					55-20 (in laboratory) 30-20 (terminal)		1-15 (1-5 in laboratory) (10-15 in open) 0.5-1 (terminal)	110-120	Energy peak - 30 kHz Indoors - pulses lasting 4 msec or less; flying in straight lines at several meters above the ground their pulses almost always lasted 10 msec or longer Out of doors - pulses are CF during major part of duration; frequency change onl, 8.2 kHz over 8.6 msec (outdoors) and drops from 50-25 kHz during 2 msec (laboratory) Temperate	Peff and Simmons 1971 Simmons and Vernon 1971 Simmons 1971, 1969 Mogus 1967 Griffin 1962, 1958, 1953 Webster and Brazier 1968
Glossophaga longirostris	FM					112-56	3.1-6.1	0.5-2		Tropical	A. Pye 1967
Glossophaga soricina leachii	FM					93-60	3.7-5.7	0.9 (0.7-1)		Strong 2nd harmonic	Novick 1963 Griffin and Novick 1955
Lasiurus borealis	FM					95-40 (search) 55-35 (terminal)	3.4-8.6 6.2-10	3-0.3 (in laboratory) 6-11 (in open)			Webster and Brazier 1968 Webster 1963 Griffin 1953
Leptonycteris nivalis	FM					100-50 (2nd harmonic)	3.4-6.9	2-8		Tropical	Novick 1963
Lonchophylla robusta	CF	25-108	13.8-3.2	0.5-2.7	~80					Many harmonics Tropical	Griffin and Novick 1955

(a) C = 344mm/msec

I
SIGNAL CHARACTERISTICS

SPECIES	SIGNAL FORM	CONTINUOUS FREQUENCY: FREQUENCY, kHz	CONTINUOUS FREQUENCY: $\lambda^{(a)}$, mm	CONTINUOUS FREQUENCY: DURATION, msec	CONTINUOUS FREQUENCY: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	FM: FREQUENCY SWEEP, kHz	FM: $\Delta\lambda^{(a)}$, mm	FM: DURATION, msec	FM: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	REMARKS	REFERENCES
Lonchorina aurita	CF	12 kHz	28.7	1-5.5						2nd and 3rd harmonics very prominent Tropical	Griffin and Novick 1955
Macrophyllum macrophyllum	CF	21-30	16.4-11.5	0.9-1.9						Tropical	Griffin and Novick 1955
Macrotus mexicanus	FM					40-26	8.6-13.2	2.5-3.5		Signal accompanied by strong 2nd harmonic Tropical	Novick 1963
Mormo[illegible]s megalophylla	FM					48-37	7.2-9.3	4-5		Tropical	A. Pye 1967
Myotis lucifugus	FM					100-40 (search) 35-25 (terminal)	3.4-8.6 9.8-13.6	3-5 0.5-0.1	95-115	Temperate	Griffin 1958 Novick 1971 Griffin 1962 Webster and Brazier 1968 Cahlander 1967 Mogus 1967
Natalus mexicanus	FM					85-50	4-6.9	2.3-2.5		Strong 2nd harmonic Tropical	Novick 1962
Noctilio labialis minor (Dirias albiventer minor)	FM					62-41	5.5-8.4	4.1-13	115-120	Tropical	Griffin and Novick 1955

(a) C = 344mm/msec

I
SIGNAL CHARACTERIS\ 'S

SPECIES	SIGNAL FORM	CONTINUOUS FREQUENCY				FM				REMARKS	REFERENCES
		FREQUENCY, kHz	$\lambda^{(a)}$, mm	DURATION, msec	SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	FREQUENCY SWEEP, kHz	$\Delta\lambda^{(a)}$, mm	DURATION, msec	SPL, dB re 0.0002 $\frac{dyne}{cm^2}$		
Noctilio leporinus	Mixed	60	5.7	3.7	125	60-30	5.7-11.4	*3.7		Captive, flying in outdoor cage *1 msec terminal	Suthers 1965
	CF	60	5.7	6.9-8.9							
	Mixed			7.1				7.1		Wild - duration twice that of caged	Mogus 1967
	CF			13.8						Emits pulses in triplets: mixed, CF, mixed	
										Omits CF in terminal phase of capture	Griffin 1958
										Does not shorten pulse during wire avoidance	Suthers 1967
										Tropical	Griffin and Novick 1955
											Pye 1966
Phylloderma stenops	FM					70-35	4.9-9.8	0.8-2		Tropical	A. Pye 1967
Phyllostomus discolor	FM					50-25	6.9-13.8	0.5-4		Multiple harmonics	A. Pye 1967
										Tropical	
Phyllostomus hastatus panamanensis	FM					65-25	5.3-13.8	0.5-4	75-90	Several overlapping, harmonically related sweeps	Peff and Simmons 1971
										Energy peak of 35-40 kHz	Simmons 1971
										Tropical	Grinnell 1970
											Griffin and Novick 1955
											A. Pye 1967
Pizonyx vivesi	FM					40-20	8.6-17.2	3		Pulses recorded during flight relatively constant in frequency, from 20-27 kHz	Suthers 1967
										Duration does not normally shorten significantly with increasing PRR	Webster and Brazier 1969
										Temperate	

(a) C = 344mm/msec

I
SIGNAL CHARACTERISTICS

SPECIES	SIGNAL FORM	CONTINUOUS FREQUENCY: FREQUENCY, kHz	CONTINUOUS FREQUENCY: $\lambda^{(a)}$, mm	CONTINUOUS FREQUENCY: DURATION, msec	CONTINUOUS FREQUENCY: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	FM: FREQUENCY SWEEP, kHz	FM: $\Delta\lambda^{(a)}$, mm	FM: DURATION, msec	FM: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	REMARKS	REFERENCES
Plecotus rafinesquii	FM					80-25 (search ?) 45-25 (terminal?)	4.3-13.8 7.6-13.8	4 1	85	Emits from nostrils or mouth Temperate	Mogus 1967 Griffin, McCue, Grinnell 1963 Grinnell 1963 Griffin 1958 Griffin and Grinell 1958
Plecotus townsendii	FM					80-20	4.3-17.1	2-5 (search) 0.3-0.5 (terminal)	60-70	Temperate	Grinnell 1963
Pteronotus davyi	Mixed	39 (1st harmonic) 78 (2nd harmonic)	8.8 4.4	3.9-5 (search) 1-1.25 (terminal)		39-31.5 78-63	8.8-10.9 4.4-5.5	3.4 (search) 1.25-1.0 (terminal)		Strong 2nd harmonic Tropical	Novick 1971, 1965, 1963 Grinnell 1970 Mogus 1967
Pteronotus suaprensis suaprensis	CF Mixed	~25 52 (2nd harmonic)	13.8 6.6	2.2 1.5		52-42 (2nd harmonic)	6.6-8.2	1.5		2nd-5th harmonics Tropical	Grinnell 1970 Griffin and Novick 1955
Rhynchiscus naso (Rhynchonycteris naso)	CF	90-94 (2nd harmonic)	3.8-3.7	4-6.8						Tropical	Griffin and Novick 1955

(a) c = 344cm/msec

I

SIGNAL CHARACTERISTICS

SPECIES	SIGNAL FORM	CONTINUOUS FREQUENCY: FREQUENCY, kHz	CONTINUOUS FREQUENCY: $\lambda^{(a)}$, mm	CONTINUOUS FREQUENCY: DURATION, msec	CONTINUOUS FREQUENCY: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	FM: FREQUENCY SWEEP, kHz	FM: $\Delta\lambda^{(a)}$, mm	FM: DURATION, msec	FM: SPL, dB re 0.0002 $\frac{dyne}{cm^2}$	REMARKS	REFERENCES
Saccopteryx bilineata	CF FM	20-33	17.2-10.4	3.5-15		20-18 (1st harmonic) 40-36 (2nd harmonic)	17.2-19.1	8		Multiple harmonics. 2nd dominant Tropical	Grinnell 1970 Griffin and Novick 1955 A. Pye 1966
Sturnira lilium	FM					96-50	3.6-6.9	1-1.3		Tropical	A. Pye 1967
Sturnira tildae	FM					96-50	3.6-6.9	1-1.3		Tropical	A. Pye 1967
Tadarida brasiliensis mexicana	FM					45-25	7.6-13.8	1.4-4.2		Emits pulse doublets during approach to obstacle	Vernon and Peterson 1965
Uroderma bilobatum	CF	69-88	5-4	1-2						Tropical	Griffin and Novick 1955
Vampyrops helleri	FM					108-72	3.2-4.8			Tropical	A. Pye 1967
Vampyrum spectrum	FM					110-65	3.1-5.3	1.8-1.3 (search) 0.5 (terminal)		Tropical	Bradbury 1970

(a) C = 344mm/msec

II
SONAR CHARACTERISTICS

SPECIES	FLYING SPEED, m/sec	PRR, sec⁻¹	CONTINUOUS FREQUENCY	FM			REMARKS	REFERENCES
			BEAMWIDTH, deg	ΔBEAMWIDTH, deg	RANGE RESOLUTION, mm Δt	Δf		
Chilonycteris parnellii mexicana	4.5	~14 (search) 80-100 (terminal)					Increases pulse duration during early pursuit to increase pulse-echo overlap to ~17 to 20 msec. Decreases pulse duration during later pursuit to reduce pulse-echo overlap to ~5 msec at capture	Novick and Vaisnys 1963 Novick 1965
Chilonycteris psilotis	1.75	17-18 (search) ~170 (terminal)			~55	~1	Maintains 1-1.5 msec pulse-echo overlap during pursuit	Novick 1965, 1963
Chilonycteris rubiginosa (chilonycteris parnellii)	3	to 125		22 (-3 dB) (calculated) (2nd harmonic)			Assumed simple piston radiator in infinite baffle; f=56 kHz	Schnitzler 1968 Mogus 1970
Eptesicus fuscus	3-4	4-10 (search) 200 (terminal)		55-65 (-3 dB) 42 (-3 dB) (calculated)	~58 (search) 7.5 (terminal)	0.4-0.8 3.5	Assumed simple piston radiator	Peff and Simmons 1971 Mogus 1967, 1970 Webster and Brazier 1968
Lasiurus borealis	4-12	5-15 (search) to 240 (terminal)			40-50 (search) 5-8.5 (terminal)	~0.3 0.5		Webster and Brazier 1969, 1968 Webster 1963
Myotis lucifugus	0.5-3 (search/ pursuit) 0.5-1 (capture)	10-20 (search) 100-200 (terminal)		25-50 (-3 dB) (search; calculated) ~70 (-3 dB) (terminal; calculated)	>34 5-17	~0.4 3.5	Tend to reduce average flight speed in laboratory	Griffin 1958 Webster and Brazier 1968, 1965 Mogus 1970, 1967 Cahlander, McCue and Webster 1964

II
SONAR CHARACTERISTICS

SPECIES	FLYING SPEED, m/sec	PRR, sec⁻¹	CONTINUOUS FREQUENCY	FM			REMARKS	REFERENCES
			BEAMWIDTH, deg	ΔBEAMWIDTH, deg	RANGE RESOLUTION, mm Δt	Δf		
Noctilio leporinus	5-8	1c-30 (search) 200 (terminal)	20 (-3 dB) (calculated)	20-34 (-3 dB) (calculated)	17 (terminal)	0.6	Assumed simple piston radiator in infinite baffle; f=50 kHz; Δf=50-30 kHz	Suthers 1965 Bloedel 1955 Mogus 1967, 1970 Griffin 1958
Phyllostomus hastatus panamanensis				~45 (-3 dB)	8-17	~0.5		Peff and Simmons 1971 Simmons 1971
Pizonyx vivesi		10-20 (search) 30-200 (terminal)			~50	0.7	High PRR's unusual; average 30 to 50	Suthers 1967 Webster and Brazier 1969
Plecotus ranfinerquii	(see remarks)	15 (search) ~65 (terminal)			68 17	~0.8	Can hover in flight	Mogus 1967 Webster and Brazier 1963
Pteronotus davyi	1.25	~10 (search) 200 (terminal)			55-85 (search) ~17 (terminal)	2-1	Signal has strong 2nd harmonic Maintains 1-3 msec pulse-echo overlap during pursuit	Novick 1965, 1963

III

AUDIOMETRIC DATA

SPECIES	AUDIOGRAM[a]	FREQUENCY RANGE, kHz	MAXIMUM SENSITIVITY		REMARKS	REFERENCES
			FREQUENCY, kHz	SPL, dB re 0.0002 dyne/cm^2		
Carollia perspicillata	Electrophysiological (N_4)	10-150	80	~25		Grinnell 1970
Chilonycteris parnellii	Electrophysiological (CM)	23-75	61.8		Roll-offs of 150-200 dB/kHz	Pollak, Henson, and Novick 1972
Chilonycteris rubiginosa	Electrophysiological (N_4)	10-130	63	5	Sharply tuned to frequencies in 2nd harmonics of orientation pulses from 62-65 kHz down to ~55 kHz. Roll-offs of 30 dB/0.2 kHz, 55 dB/0.5 kHz	Grinnell 1970
Desmodus rotundus murinus	Electrophysiological (CM)	0.1-100	10-60		Removal of pinna and tragus had negligible effect upon response or sensitivity	Vernon and Peterson 1966
Eptesicus fuscus	Behavioral; operant conditioning	2.5-100	10-25 50-70	~5	Excellent agreement between behavioral and electrophysiological (N_4) measurements of audiogram	Dalland 1965 Dalland, Vernon, and Peterson 1967 Henson 1971
Molossus milleri	Electrophysiological (N_4)	<10-60	35-40			Henson 1967 Henson 1971

[a] BEHAVIORAL; TASK ELECTROPHYSIOLOGICAL

III
AUDIOMETRIC DATA

SPECIES	AUDIOGRAM[c]	FREQUENCY RANGE, kHz	MAXIMUM SENSITIVITY		REMARKS	REFERENCES
			FREQUENCY, kHz	SPL, dB re 0.0002 dyne/cm^2		
Myotis lucifugus	Electrophysiological (CM)	0.7-100	12 and 35 (12-60)			Vernon, Dalland, and Wever 1966
	Electrophysiological (N_4)	10-170	30-50	~25		Grinnell 1963
	Behavioral; operant conditioning	12-120	40 (20-60)	10		Dalland 1965
Phyllostomus hastatus panamanensis	Electrophysiological (N_4)	10-90	30-35 50-55	~25		Grinnell 1970
Plecotus townsendii	Electrophysiological (N_4)	10-100	15-25 50-65	0-5	Two regions of equally low threshold, one near or slightly below the range of fundamental emitted frequencies, and a second at the second harmonic of the orientation sounds	Grinnell 1963
Pteronotus suapurensis suapurensis	Electrophysiological (N_4)	10-140	45-55	10-20		Grinnell 1970
Saccopteryx bilineata	Electrophysiological (N_4)	10-120	40-45	5-20	Roll-offs 10-100 dB/0.01 Δf; single units (neurons), 500-1500 dB/octave	Grinell 1970
Tadarida brasiliensis mexicana	Electrophysiological (CM)	0.7-100	10-40			Henson 1971, 1967
Tadarida molassa	Electrophysiological (N_4)	0.1-45	11-17			Henson 1971, 1967

[c]BEHAVIORAL; TASK
ELECTROPHYSIOLOGICAL

IV
DETECTION/DISCRIMINATION DATA

SPECIES	TARGET/OBSTACLE; DETECTION/DISCRIMINATION					SIGNAL; DETECTION, DISCRIMINATION, LOCALIZATION				REMARKS	REFERENCES
	FORM/ MATERIAL	SIZE, cm	TASK	DISTANCE, cm	PERFORMANCE	TECHNIQUE[c]	SIGNAL FORM	TASK	PERFORMANCE		
Artibeus jamaicensis palmarum	metal wire barrier (60 cm separation)	0.0175 diam	avoidance		72%						Griffin and Novick 1955
Carollia perspicillata	metal wire barrier (30 cm separation)	0.0175 diam	avoidance		56%						Griffin and Novick 1955
Chilonycteris parnellii mexicana	insects, fruitflies	0.2 (wing-span)	detect/ capture	3.8						Assumed detection range based on calculated pulse-echo overlap	Novick and Vaisnys 1964 Novick 1965
Chilonycteris psilotis	insects, fruitflies	0.2 (wing-span)	detect/ capture	40-70						Assumed detection range based on calculated pulse-echo overlap	Novick 1965
Eptesicus fuscus	triangles, plastic	7-10, base 3.5-5, height	discrimination, size	30	75% @ Δ area ~ 17% Δ intensity ~ 1.5-3 dB					Discrimination likely mediated by echo intensity differences (proportional to Δ area)	Simmons and Vernon 1971
	triangles, plastic	6Bx12H versus 12Bx6H	discrimination, shape	30	>80%						
	triangles, plastic	10 cm, base 5 cm, height	discrimination, distance	30, 60	75%, Δd=1.2 cm (Δt:70-75 μsec)					Resolution apparently independent of distance. Performance compares favorably with estimate based on autocorrelation of emitted signal	Simmons and Vernon 1971 Simmons 1971
	pebbles	1-2 diam	detection	200							Griffin 1953
	spheres, nylon	1.9 diam	horizontal angle resolution	30	75%, Δθ=6°-8°						Peff and Simmons 1971

[c] BEHAVIORAL, TASK
ELECTROPHYSIOLOGICAL

IV
DETECTION/DISCRIMINATION DATA

SPECIES	TARGET/OBSTACLE; DETECTION/DISCRIMINATION: FORM/MATERIAL	SIZE, cm	TASK	DISTANCE, cm	PERFORMANCE	SIGNAL; DETECTION, DISCRIMINATION, LOCALIZATION: TECHNIQUE[c]	SIGNAL FORM	TASK	PERFORMANCE	REMARKS	REFERENCES
Glossophaga	metal wire barrier (30 cm separation)	0.0175	avoidance		89%						Griffin and Novick 1955
Lasurius borealis										Seem able to evaluate position of maneuvering target without apparent head following	Webster 1965
Macrotus mexicanus	metal wire barrier (40 cm separation)	0.038 diam 0.027 diam	avoidance		80% 77%						Grummon and Novick 1963
Myotis lucifugus	sphere, nylon	0.16 0.32	detection	~60 90-110							
	mealworm	0.2-0.3 diam 1.5-2.5 long	discrimination (versus spheres)		30% versus spheres of comparable echo intensity*; ~95% versus others *0.4-0.8 cm diam					Are able to select individual target out of cluster (n≦16) Are capable of achieving localization accuracies of 1 cm^3	Webster and Brazier 1965
	metal wire barrier (30 cm separation)	0.3 0.107 0.065 0.046 0.028 0.018	detection avoidance	215 185 150 120 105 90	80% 75%						Grinnell and Griffin 1958
	discs, bakelite	1.6 1.25 diam 0.3 thick	discrimination (versus mealworms)		catches: 90% mealworms versus 20-40% discs						Griffin, Friend, and Webster 1965

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ELECTROPHYSIOLOGICAL

IV
DETECTION/DISCRIMINATION DATA

SPECIES	TARGET/OBSTACLE; DETECTION/DISCRIMINATION					SIGNAL; DETECTION, DISCRIMINATION, LOCALIZATION				REMARKS	REFERENCES
	FORM/MATERIAL	SIZE, cm	TASK	DISTANCE, cm	PERFORMANCE	TECHNIQUE[c]	SIGNAL FORM	TASK	PERFORMANCE		
Myotis lucifugus (Cont'd)	disks, metal	0.63 0.95 1.25 1.6 diam 0.05 thick	discrimination (versus mealworms)		catches: 80% mealworm versus 30%, 0.95 20%, 1.25						Griffin, Friend, and Webster 1965
	insects, fruitflies	0.5-3 mg	detection, capture	50-100						Echo SPL: ~30 dB re 0.0002 dyne/cm² at 50 cm, bat to fruitfly	Griffin, Webster, and Michael 1960
	mosquitoes	~2.2 mg								Bats often slow down on approaching wire barriers, but insects are intercepted at flight speeds ~1 m/sec Reflectance of fruitfly corresponds roughly to that of 0.2 cm diam sphere	
	metal wire barrier (45 cm separation)	0.054 0.028	avoidance		~88% ~88% (in quiet and in noise)						Griffin 1958
	metal wire barrier	0.121 0.026 0.012	avoidance		82% 52% 39%						Curtis, 1952
						electrophysiological	tone burst	discrimination, frequency	Δf:0.5-1 kHz, f:50-100 kHz		Grinnell 1963
						electrophysiological	tone burst	discrimination, intensity	ΔI:0.2-0.5 dB		
						electrophysiological	tone burst	discrimination, time		Are capable of complete temporal resolution down to intervals <1 msec	

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IV
DETECTION/DISCRIMINATION DATA

SPECIES	TARGET/OBSTACLE; DETECTION/DISCRIMINATION: FORM/MATERIAL	SIZE, cm	TASK	DISTANCE, cm	PERFORMANCE	SIGNAL; DETECTION, DISCRIMINATION, LOCALIZATION: TECHNIQUE[c]	SIGNAL FORM	TASK	PERFORMANCE	REMARKS	REFERENCES
Noctilio leporinus	cube, fish muscle	1-2	detection of cube partially exposed at water surface	130-150	~100%						Suthers 1965
	upwelling, water	5-10, high 10-15 diam	detection and dipping for fish cube		85%						
	metal wire	0.035 0.021	detection of 0.5 cm length protruding above water surface	~60	90% 80%					Are extremely skillful at detecting echoes from tiny surface disturbances	
	metal wire	0.13 and 0.09	discrimination of single 0.13 cm wire from pair of 0.09 cm wires protruding 0.05 cm above water surface		~80%						
	metal wire barrier (55 cm separation)	0.051 0.021	avoidance	150 130	76% 60%					Emitted longer pulses when approaching 0.021 cm wires than when approaching 0.051 cm wires	Suthers 1967

(c) BEHAVIORAL; TASK
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IV
DETECTION/DISCRIMINATION DATA

SPECIES	TARGET/OBSTACLE, DETECTION/DISCRIMINATION					SIGNAL; DETECTION, DISCRIMINATION, LOCALIZATION				REMARKS	REFERENCES
	FORM/ MATERIAL	SIZE, cm	TASK	DISTANCE, cm	PERFORMANCE	TECHNIQUE[c]	SIGNAL FORM	TASK	PERFORMANCE		
Phyllostomus hastatus panamanensis	triangles, plastic	10, base 5, height	discrimination, target distance	60	Δd, ~1.2 cm (75%)					Echo level: 0.05 dyne/cm^2. Performance compares favorably with estimate based on auto-correlation of emitted signal	Simmons 1971
	spheres, nylon	1.9 diam	horizontal angle resolution	30	4°-6°						Peff and Simmons 1971
Pizonyx vivesi	metal wire barrier (55 cm separation)	0.051 0.021	avoidance		83% 51%					Average distance of detection: 0.051:110 cm 0.021: 70 cm	Suthers 1967
Plecotus townsendii (plecotus rafinesquii)	metal wire barrier (45 cm separation)	0.054 0.028	avoidance		91% 69%						Griffin 1958
	metal wire barrier (45 cm separation)	0.028	avoidance		80% (in quiet) 50-60% (in noise)					Estimated echo level @ 10 cm from wire: 24 dB re 0.0002 dyne/cm^2 Noise SPL: +80-90 (15-55 kHz)	Griffin and Grinnell 1958
	metal wire barrier (45 cm separation)	0.054	avoidance		~85% (in noise; 10-50 kHz bandwidth) 30-40% (in noise; 10-90 kHz bandwidth)					Indicates use of higher (2nd) harmonic of signal (to overcome noise masking)	Griffin, McCue, and Grinnell 1963
						electrophysiological (N_4)	tone burst	detection, intensity difference	ΔI:0.2-0.5 dB		Grinnell 1963
						electrophysiological (N_4)	tone burst	detection, frequency difference	ΔF:0.005f to 0.01f		
						electrophysiological (N_4)	tone burst	detection, time difference	Δt:<1 msec		

[c] BEHAVIORAL; TASK
ELECTROPHYSIOLOGICAL

IV
DETECTION/DISCRIMINATION DATA

SPECIES	TARGET/OBSTACLE; DETECTION/DISCRIMINATION: FORM/MATERIAL	SIZE, cm	TASK	DISTANCE, cm	PERFORMANCE	SIGNAL; DETECTION, DISCRIMINATION, LOCALIZATION: TECHNIQUE[c]	SIGNAL FORM	TASK	PERFORMANCE	REMARKS	REFERENCES
Pteronotus davyi	insects, fruitflies	0.2 (wing-span)	detect/capture	10-85						Assumed detection range based on calculated pulse-echo overlap	Novick 1963 Novick 1965
Vampyrum spectrum	spheres, rubber	15 and 6, diam	discrimination, shape		~85%, 15 cm sphere versus cylinder						Bradbury 1970
	cylinder, wood	10.5 L x 2.5 diam			~80%, 6 cm sphere versus cylinder						
	sphere, lucite	3.08 diam	discrimination, shape	50-150	60%-80%					One bat used frequency responses of targets for discrimination; other used overall amplitude differences	
	spheroid, lucite	ratio 5/3, interfocal distance: 2.1									

[c] BEHAVIORAL; TASK
ELECTROPHYSIOLOGICAL

V
HABITAT/PREY/BIOLOGY

SPECIES	SIZE	HABITAT	BEHAVIOR	PREY	REMARKS	REFERENCES
Anoura geoffroyi	14 g	forest (tropical and arid) neotropical		fruit and insects		Pye 1967 Walker 1968
Artibeus jamaicensis palmarum	55-70 g	neotropical		fruit		Novick 1963 Griffin and Novick 1955 Pye 1967 Griffin 1958 Walker 1968
Artibeus lituratus	45-90 g	neotropical		fruit, nuts		Walker 1968
Balantiopteryx plicata	5-9 g	arid to semitropical zones of New World	Slow, erratic flight	insects		Walker 1968
Carollia perspicillata	14-20 g pinnae: 17 mm long 8 mm wide	neotropical	Swift fliers	fruit		Griffin and Novick 1955 Grinnell 1962 Walker 1968
Centurio senex	17-28 g	neotropical	Jerky flight	fruit		Pye 1967 Walker 1968

V
HABITAT/PREY/BIOLOGY

SPECIES	SIZE	HABITAT	BEHAVIOR	PREY	REMARKS	REFERENCES
Chilonycteris personata	~20 g	neotropical		insects		Novick 1963 Griffin 1958 Walker 1968
Chilonycteris rubiginosa (Chilonycteris parnellii)	18-24 g pinnae: 22 mm long 9 mm wide	rain forest neotropical		insects		Novick 1963 Griffin and Novick 1955 Pye 1967 Grinnell 1962 Walker 1968
Chiroderma villosum	to 30 g			fruit		Pye 1967
Desmodus rotundus murinus	15-50 g pinnae: 15.5 mm long 9 mm wide	neotropical	Slow, silent flight near ground	Large, not very elusive prey. Feeds exclusively on vertebrate blood		Novick 1963 Vernon and Peterson 1966 Pye 1967 Grinnell 1962 Walker 1968

Y
HABITAT/PREY/BIOLOGY

SPECIES	SIZE	HABITAT	BEHAVIOR	PREY	REMARKS	REFERENCES
Eptesicus fuscus	12-24 g pinnae: 14.5 mm long 8 mm wide		Rapid, strong, steady flight. Feed near ground	insects		Grinnell 1962 Walker 1968
Glossophaga sp.	8-15 g	wooded country and arid lowlands	Fly at great speed. Hover to drink nectar	fruit and insects		Pye 1967 Griffin and Novick 1955 Walker 1968
Lasurius borealis	6-30 g	over woods and along water courses	Strong fliers. Feed 6-15 m above ground	insects (moths)		Gould 1955 Walker 1968
Leptonycteris nivalis	18-30 g	arid, open country		fruit		Novick 1963 Walker 1968
Lonchophylla robusta	45-60 g	neotropical		fruit, nectar, insects		Walker 1968
Lonchorhina aurita	10-16 g	neotropical				Griffin and Novick 1955 Walker 1968
Macrophyllum macrophyllum	6-9 g	rain forest neotropical				Griffin and Novick 1955 Griffin 1958 Walker 1968

V
HABITAT/PREY/BIOLOGY

SPECIES	SIZE	HABITAT	BEHAVIOR	PREY	REMARKS	REFERENCES
Macrotus mexicanus	12-20 g pinnae: 26 mm long 13 mm wide	arid lowlands	Feed in flight on ground	insects		Novick 1963 Grummon and Novick 1963 Grinnell 1962 Walker 1968
Micronycteris hirsuta	12 g	neotropical		fruit		Pye 1967 Walker 1968
Mollosus milleri	to 95 g	neotropical		insects		Walker 1968
Mormoops megalophylla	12-20 g	hunt over land and water just above surface		insects		Pye 1967 Walker 1968
Myotis lucifugus	5-14 g pinnae: 14 mm long 7 mm wide	wooded and open areas worldwide	Erratic and fast fliers	insects (flys, moths, beetles, mosquitoes)		Grinnell 1962 Griffin 1958 Walker 1968
Natalus mexicanus	to 10 g	neotropical	Fluttering, mothlike flight	insects		Novick 1962 Walker 1968

V
HABITAT/PREY/BIOLOGY

SPECIES	SIZE	HABITAT	BEHAVIOR	PREY	REMARKS	REFERENCES
Noctilio labialis minor	15-22 g	neotropical	Catch insects on water surface	insects (water beetles)		Griffin and Novick 1955 Walker 1968
Noctilio leporinus	30-70 g pinnae: 26 mm long 9 mm wide	streams, lakes, and ocean neotropical	Slow, deliberate flight. Gaffs fish by trailing feet through water	fish and insects		Grinnell 1962 Bloedel 1955 Griffin and Novick 1955 Griffin 1958 Walker 1968
Phylloderma stenops	20-25 g	neotropical				Pye 1967 Walker 1968
Phyllostomus discolor	20-40 g	neotropical		fruit, nectar, pollen		Walker 1968
Phyllostomus hastatus panamanensis	70-100 g pinnae: 28 mm long 12 mm wide	neotropical	Straight, rapid fliers	omnivorous (small animals--rodents, birds, bats--insects, fruit)		Grinnell 1970 Griffin 1958 Griffin and Novick 1955 Pye 1967 Grinnell 1962 Walker 1968

V
HABITAT/PREY/BIOLOGY

SPECIES	SIZE	HABITAT	BEHAVIOR	PREY	REMARKS	REFERENCES
Pizonyx vivesi		Gulf of California	(see remarks)	crustaceans and fish	Assumed bat gaffs fish by trailing feet in water	Bloedel 1955 Webster and Brazier 1968, 1969 Walker 1968
Plecotus townsendii (plecotus rafinesqii)	10 g pinnae: 37 mm long 12 mm wide	temperate regions of New World	Versatile flyers; can hover in flight. Hunt along solid surfaces	insects (moths)		Grinnell 1962 Walker 1968
Pteronotus davyi	7-10 g	near water neotropical	Swift flight near ground	insects		Novick 1965 Walker 1968
Pteronotus suapurensis		feed along streams and rivers in wooded areas neotropical	Unusually skillful fliers; capable of hovering in flight	insects		Grinnell 1970 Walker 1968
Rhynchiscus naso (Rhynchonycteris naso)	2-4 g	near water neotropical	Slow, steady flight just above water surface	insects		Griffin and Novick 1955 Griffin 1958 Walker 1968
Saccopteryx bilineata	5-6 g pinnae: 15 mm long 7.5 mm wide	neotropical	Fly in open spaces	insects (beetles and moths)		Griffin and Novick 1955 Grinnell 1962 Walker 1968

V
HABITAT/PREY/BIOLOGY

SPECIES	SIZE	HABITAT	BEHAVIOR	PREY	REMARKS	REFERENCES
Sturnira sp.	16-20 g	forest (tropical and arid) neotropical		fruit		Pye 1967 Walker 1968
Tadarida brasiliensis mexicana	10-15 g pinnae: 9.5 mm long 7.5 mm wide	open country	High flyer	insects		Vernon and Peterson 1965 Grinnell 1962 Walker 1968
Uroderma bilobatum	13-21 g	neotropical		fruit		Walker 1968
Vampyrops helleri	12-15 g	watercourses in tropical forests neotropical		fruit		Walker 1,68
Vampyrum spectrum	145-190 g	neotropical		small animals (birds, rodents, bats), insects, fruit		Walker 1968

APPENDIX III

TABULATIONS OF BIOLOGICAL SONAR DATA FOR WHALES, DOLPHINS, AND PORPOISES

I

SIGNAL CHARACTERISTICS

SPECIES	SIGNAL-FORM	PEAK FREQUENCY kHz	BANDWIDTH[a] kHz	DURATION msec	SPL dB re 1 µbar	REMARKS	REFERENCES
Delphinus delphis	pulse (click)	30-60	to 150	0.05-0.25	40		Evans and Evans 1971 Evans 1972
Eschrichtius gibbosus	pulse	2-3 kHz	to 12*	1-1.5	52	*Upper limit of sonagram	Poulter 1968 Evans and Evans 1971
Globicephala melaena	pulse (click)	3	~5*	0.5		*~10% threshold on Fourier power spectrum	Busnel et al. 1971
Globicephala scammoni	pulse (click)	~3	to 16* to 100	0.5-2 0.25-2	 80	*Upper limit of sonagram	Norris 1969 Evans and Evans 1971 Evans 1972
Inia geoffrensis	pulse (click)	60-75	≥150*	0.015-0.1	66	*10% threshold on Fourier power spectrum	ARL 1970
Lagenorhynchus australis	pulse (click)	~1 ~5-6	<2 to 16*	1.5-3 0.8-1	-20	Limited hydrophone bandwidth (LC-34); limited recorder bandwidth (30 kHz) *Upper limit of sonagram	Schevill and Watkins 1971
Lagenorhynchus obliquidens	pulse		to 80	0.25-1	70		Evans 1972
Orcinus orca	pulse (click)	~12	to 35*	0.1-0.5	~80	*10% threshold on Fourier power spectrum	ARL 1971

[a]DEFINITION; ANALYSIS

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I
SIGNAL CHARACTERISTICS

SPECIES	SIGNAL FORM	PEAK FREQUENCY kHz	BANDWIDTH(a) kHz	DURATION msec	SPL dB re 1 µbar	REMARKS	REFERENCES
Phocoena phocoena	pulse (click)	2	~4*	0.5-5	25-30	Limited bandwidth instrumentation: f≤10 kHz *Upper limit of sonagram	Schevill, Watkins, and Ray 1969
			to ~100	0.02-1.5		Instrumentation capabilities unknown	
	pulse	140-150	100->160*	0.1	40	Two hydrophones: LC-32, B&K 8100 *Upper limit of spectrum analyzer trace	Dubrovskii, Krasnov, and Titov 1971 Møhl and Andersen 1972
Phocoenoides dalli	pulse (click)	1-2	to 14*	0.5-1.5		Limited hydrophone bandwidth (LC-32) *Limit of trace on sonagram	Ridgway 1966 Evans and Evans 1971 Evans 1972
Physeter catadon	pulse (click)	~6	to 15**	0.75-5	to 84**	*Upper limit of sonagram *Limited bandwidth instrumentation **1/3 octave, 1 kHz band; system bandwidth: 4 kHz	Dunn 1969 Backus and Schevill 1966 Evans 1972
Platanista gangetica	pulse (click)	20-40	to 150*	0.075-0.15	40	*Limit of trace on sonagram: 100 kHz	Herald et al. 1969 Evans 1972
Platanista indi	pulse (click)	50-60	to 100*	~0.02		Limited hydrophone bandwidth (LC-32): limited recorder bandwidth (30 kHz) *Upper frequency limit of instrumentation	Pilleri, Kraus, and Gihr 1971
Pseudorca crassidens	pulse (click)		to 30*	0.2-0.5		*Upper frequency limit of instrumentation	Busnel and Dziedzic 1966

(a)DEFINITION; ANALYSIS

I

SIGNAL CHARACTERISTICS

SPECIES	SIGNAL FORM	PEAK FREQUENCY kHz	BANDWIDTH[o] kHz	DURATION msec	SPL dB re 1 μbar	REMARKS	REFERENCES
Stenella attenuata	pulse		to 150	0.075-0.2			Evans and Evans 1971
Stenella styx	pulse		to 22			Limited bandwidth instrumentation	Busnel, Pilleri, and Frazer 1968
Steno bredanensis	pulse (click)	40-80	to 208*	0.05-0.25		*Sonagram	Norris and Evans 1967; Evans and Evans 1971; Evans 1972
Tursiops truncatus	pulse (click)	30-60	to 130*	0.02-0.1	75-110	*10% threshold on Fourier power spectrum	ARL/NUC 1969
Tursiops truncatus (Black Sea)	pulse (click)	~15		0.05-0.5		Instrumentation capabilities unknown	Airapetianz et al. 1971

[o] DEFINITION; ANALYSIS

II
SONAR CHARACTERISTICS

SPECIES	SWIMMING SPEED, m/sec	PRR, /sec	BEAMWIDTH, deg	REMARKS	REFERENCES
Delphinus delphis	to 13		50-60 (60 kHz) (skull only) ~55 (80 kHz) (skull only) ~30 (100 kHz) (skull only) ~15 (100 kHz) (skull and melon)	Artificial source positioned at location of nasal plugs	Romanenko, Tomilin, and Artemenko 1965 Romanenko 1965 Walker 1968
Inia geoffrensis	~1 4-5 (burst)	to 135		Scans laterally or vertically by linear motion with abrupt right angle turns	Penner and Murchison 1970 ARL 1970 Layne 1958
Lagenorhynchus australis		to 25 (narrowband click) to 80 (broadband click)			Schevill and Watkins 1971
Orcinus orca	to 15	>250	40		ARL 1971 Evans 1972 Johannessen and Harder 1960
Phocoena phocoena		to 1000	<60, (130 kHz)		Schevill, Watkins, and Ray 1969 Møhl and Andersen 1972
Phocoenoides dalli	>9	to 30*		*Click burst produced in captivity	Ridgway 1966

X
SONAR CHARACTERISTICS

SPECIES	SWIMMING SPEED, m/sec	PRR, /sec	BEAMWIDTH, deg	REMARKS	REFERENCES
Physter catadon	~2	to 50, average 1-7			Backus and Schevill 1966 Dunn 1969 Walker 1968
Plantista gangetica	~2-4	20-50		Swim on side with body axis inclined ~10° to bottom	Herald et al. 1969 Pilleri 1970
Platonista indi		to 125			Pilleri, Kraus, and Gihr 1971
Pseudorca crassidens		to 140			Busnel and Dziedzic 1966
Stenella styx		~60			Busnel, Pilleri, and Fraser 1968
Steno bredanensis		to >100	20, (-3 dB) ~4, (200 kHz) ~10, (150 kHz) ~20, (100 kHz)		Norris and Evans 1967 Evans 1967
Tursiops truncatus	~9	to 600	~38, (70 kHz) (horizontal: skull only) ~22, (70 kHz) (vertical: skull only) ~25-30 (horizontal: -3 dB)	-3 dB 0° tilt re rostrum axis	Evans, Sutherland, Beil 1964 Evans and Powell 1967 Evans 1972

III
AUDIOMETRIC DATA

SPECIES	AUDIOGRAM[a]	FREQUENCY RANGE, kHz	MAXIMUM SENSITIVITY: FREQUENCY, kHz	MAXIMUM SENSITIVITY: SPL, dB re 0.0002 dyne/cm²	MAXIMUM SENSITIVITY: AREA	REMARKS	REFERENCES
Delphinus delphis	behavioral	to 280					Bel'kovich and Solntseva 1970
Inia geoffrensis	behavioral	1-105	75-90* 30-50#	24		*Text; #Fig. 3 of reference 60 dB roll-off, 50 kHz to 100 kHz (Fig. 3 of reference).	Jacobs and Hall 1972
Orcinus orca	behavioral	0.5-31	15-25	0-10		60 dB roll-off, 25 kHz to 31 kHz	Hall and Johnson 1972
Phocoena phocoena	behavioral	1-150	8-32	~24		15 dB/octave roll-off, 40 kHz to 140 kHz; 700 dB/octave roll-off, 140 kHz-150 kHz	Andersen 1970
Stenella attenuata	electrophysiological (N_4)	10-150	50-70	5-20	lower jaw	70 dB roll-off, 70 kHz to 140 kHz	Bullock et al. 1968
Stenella caeruleoalba	electrophysiological (N_4)	10-150	50-70	5-20	lower jaw	70 dB roll-off, 70 kHz to 140 kHz	Bullock et al. 1968
Tursiops gilli	electrophysiological (N_4)			10-25	lower jaw	Dependent upon stimulus duration	Bullock et al. 1968 McCormick 1968 McCormick et al. 1970 Norris 1969
Tursiops truncatus	behavioral	0.1-150	30-80	~10		Dependent upon stimulus duration	Johnson 1966, 1968

[a] BEHAVIORAL; TASK
ELECTROPHYSIOLOGICAL

IV
DETECTION/DISCRIMINATION DATA

SPECIES	TARGET/OBSTACLE; DETECTION/DISCRIMINATION					SIGNAL; DETECTION, DISCRIMINATION, LOCALIZATION				REMARKS	REFERENCES
	FORM/ MATERIAL	SIZE, cm	TASK	DISTANCE, cm	PERFORMANCE	TECHNIQUE[c]	SIGNAL FORM	TASK	PERFORMANCE		
Delphinus delphis	3-step pyramids, styrofoam	base: 100 cm^2 each; 2nd step 49 cm^2 each; 3rd step 9 cm^2 target 1, 8.6 cm^2 target 2; steps 1.2 thick	discrimination, size (6.7% diff.)	600-800	>50%*					*Value not reported	Gurevich 1969
	squares, styrofoam	100 cm^2 versus 90.25 cm^2; 1.2 thick	discrimination, area (9.75% diff.)	600-800	>50%*						
	3-step pyramids, styrofoam ebonite	same as target 1 above	discrimination, material		~100%*						
	squares, styrofoam ebonite	100 cm^2	discrimination, material		~100%*						
	fish (bullhead) versus tube, rubber	12-17 4, diam 22, long	discrimination	150-500	83% (60 trials)						Konstantinov, Mel'nikov, and Titov 1968
	fish (bullhead)	12-17 versus 27-30	discrimination, size	260, average	88%**					**Smaller fish positive target (edible)	

[c]BEHAVIORAL; TASK
ELECTROPHYSIOLOGICAL

IV
DETECTION/DISCRIMINATION DATA

SPECIES	TARGET/OBSTACLE; DETECTION/DISCRIMINATION: FORM/MATERIAL	SIZE, cm	TASK	DISTANCE, cm	PERFORMANCE	SIGNAL; DETECTION, DISCRIMINATION, LOCALIZATION: TECHNIQUE(c)	SIGNAL FORM	TASK	PERFORMANCE	REMARKS	REFERENCES
Delphinus delphis (Cont'd)	fish (bullhead) versus fish (metal clad)	equal size	discrimination, material	300, average	~85%						
	square versus triangle, ebonite and plexiglass	100 cm^2 50 cm^2	discrimination, size and shape	800	100%						Bagdonas Bel'kovich and Krushinskaya 1970
Inia geoffrensis	wire, metal	0.26 diam 0.13 0.12 0.11	detection	≥19	100% 73% 65% ~45%						Penner and Murchison 1970
	cylinder, corprene	7.8 long 4.2 diam versus 6.6 diam	discrimination, size*		75%					*2 dB target strength difference	Evans 1972
Lagenorhynchus obliquidens	ring, plastic (hollow)	25 diam	detection	200							Evans 1972
	discs, copper versus aluminum	50 diam	discrimination, material		>50%*					*Value not reported	
Orcinus orca	ring, plastic (hollow)	25 diam	detection	500							Evans 1972

(c)BEHAVIORAL: TASK
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IV
DETECTION/DISCRIMINATION DATA

SPECIES	TARGET/OBSTACLE; DETECTION/DISCRIMINATION: FORM/MATERIAL	SIZE, cm	TASK	DISTANCE, cm	PERFORMANCE	SIGNAL; DETECTION, DISCRIMINATION, LOCALIZATION: TECHNIQUE[c]	SIGNAL FORM	TASK	PERFORMANCE	REMARKS	REFERENCES
Phocoena phocoena	wire, metal (barrier, 1 m separation)	0.05 diam 0.035 diam 0.02 diam	avoidance		≥90%* 79%* ~50%*	behavioral	tone burst, 2 kHz	detection, angular displacement of signal (MAA)	75%, 3°, median plane	*Animal blindfolded	Busnel, Dziedzic, and Andersen 1965 Busnel and Dziedzic 1967 Andersen 1970
	line, monofilament nylon (barrier, 1 m separation)	0.18 diam 0.15 diam	avoidance		85%* 72%*						
	line, 3-strand perlon (barrier, 1 m separation)	0.1 diam 0.08 diam	avoidance		>96%* 58%*						
Tursiops truncatus (Black Sea)	cylinder	11 diam 25 long versus 28 30 35 45 55 75	discrimination, length		100%, 25 versus ≥35 70%, 25 versus 30 50%, 25 versus 28	behavioral		discrimination, target range discrimination, angular separation of targets	$\Delta R \cong 1.5$ mm $\Delta\theta = 0.25°$ (horizontal) 0.8° (vertical)		Ayrapet'yants et al. 1969 Airapetiantz and Konstantinov 1971

[c]BEHAVIORAL; TASK
ELECTROPHYSIOLOGICAL

IV
DETECTION/DISCRIMINATION DATA

SPECIES	TARGET/OBSTACLE; DETECTION/DISCRIMINATION					SIGNAL; DETECTION, DISCRIMINATION, LOCALIZATION				REMARKS	REFERENCES
	FORM/ MATERIAL	SIZE, cm	TASK	DISTANCE, cm	PERFORMANCE	TECHNIQUE[c]	SIGNAL FORM	TASK	PERFORMANCE		
Tursiops truncatus (Montagu)	spheres, steel	5.4 diam 5.71 diam 6.35 diam	discrimination, size	45-60	100%, 6.35 versus 5.4 77%, 6.35 versus 5.71						Norris, Evans, and Turner 1967
	discs, metal: copper	30 diam thickness: 0.22 std 0.32 0.27 0.16	discrimination, material, thickness		75%, 0.22 versus 0.32 60%, 0.22 versus 0.27 50%, 0.22 versus 0.16						Evans and Powell 1967
	brass	0.64 0.32			100%, 0.22 versus 0.64 55%, 0.22 versus 0.32						
	aluminum	0.79 0.64 0.32			95%, 0.22 versus 0.79 97%, 0.22 versus 0.64 100%, 0.22 versus 0.32						
	cylinder, vitamin capsule	0.5 diam 1.5 long	detection	~30-60						Target lying on tank floor	Johnson 1967
	cylinders, corprene	17.8 long 4.2 diam versus 5.2 diam	discrimination, size*		85%					*1 dB target strength difference	Evans 1972
	gelatin capsule, water-filled with pebbles versus fish muscle	3.8 long 3.8 long	discrimination, material	~30-50	100%						Norris et al. 1961

(c)BEHAVIORAL; TASK
ELECTROPHYSIOLOGICAL

IV
DETECTION/DISCRIMINATION DATA

SPECIES	TARGET/OBSTACLE; DETECTION/DISCRIMINATION					SIGNAL; DETECTION, DISCRIMINATION, LOCALIZATION				REMARKS	REFERENCES
	FORM/ MATERIAL	SIZE, cm	TASK	DISTANCE, cm	PERFORMANCE	TECHNIQUE[c]	SIGNAL FORM	TASK	PERFORMANCE		
Tursiops truncatus (Montagu) (Cont'd)	discs, celltite	diff diam, 15.2 std	discrimination, size	120-180	58%, Δ diam 0.5 cm* 75%, Δ diam 0.9 cm*	behavioral	tone burst	discrimination, intensity	ΔI~1 dB	*Δ area: 6.7% and 12% Δ target strength: 0.6 dB and 1 dB	Barta 1969 Johnson 1967
	disc versus square versus triangle, celltite	15.2 diam equal area	discrimination, shape	120-180	>95%						
	fish	5-15 long	detection	500-1000							Evans 1972

[c]BEHAVIORAL; TASK
ELECTROPHYSIOLOGICAL

V
HABITAT/PREY/BIOLOGY

SPECIES	SIZE	HABITAT	BEHAVIOR	PREY	REMARKS	REFERENCES
Delphinis delphis	to 75 kg	worldwide pelagic	Very fast swimmer. Scans in rectilinear motion--up-down or sideways	fish and cephalopods found in shoals and near surface	Travel in groups from ~20 to several hundred	Walker 1968 Konstantinov, Mel'nikov, and Titov 1968
Globicephala sp.		offshore to inshore waters (seasonal) pelagic to littoral		squid, fish, cuttlefish	Schools may contain several hundred animals. During feeding schools may disperse	Walker 1968 Leatherwood, Evans, and Rice 1972 Norris 1969
Inia geoffrensis	to 125 kg	Amazon and Orinoco Rivers riverine	Scans in rectilinear motion--up-down or sideways. Hunts at leisurely swimming speed (2-3 kt)	fish (<30 cm)	Feed in small groups (3-6 animals). Habitat is muddy with minimal visibility	Walker 1968 Penner and Murchison 1970 Layne 1958
Lagenorhynchus sp.	to 150 kg	offshore to inshore waters (seasonal) pelagic to littoral	Are vigorous swimmers	fish--herring, mackeral, anchovies--crustaceans, squid	Some species feed in large schools (1000-2000 animals)	Walker 1968 Leatherwood, Evans, and Rice 1972
Orcinus orca	1000-2000 kg	worldwide, principally Arctic and Antarctic pelagic to estuarine, sometimes riverine	Apparently scans by rolling from side to side	small marine mammals (seal, walrus, porpoise) baleen whales, birds, fish, cephalopods		Walker 1968 Evans 1972 Hall and Johnson 1972 Schevill and Watkins 1966

V
HABITAT/PREY/BIOLOGY

SPECIES	SIZE	HABITAT	BEHAVIOR	PREY	REMARKS	REFERENCES
Phocoena phocoena	50-75 kg	European and African waters. littoral and sometimes riverine	Usually swims just below surface.* Feeds near bottom	fish (<30 cm), cephalopods, crustaceans	*Have been caught in fishnets at depths of 75 m	Walker 1968 Dubrovskii, Krasnov, and Titov 1971
Phocoenoides dalli	80-125 kg	pelagic	Very fast swimmer	fish and squid	Found in small groups (2-20 animals)	Walker 1968 Ridgway 1966
Physeter catadon	$30\text{-}45\times10^3$ kg	pelagic	Feed at great depths (~360 m)	squid, cuttlefish, fish (barracuda, albacore), sharks	Swim (hunt?) in groups of 15-20 animals	Walker 1968
Platanisti gangetica	20-225 kg	Ganges, Indus, and Brahmaputra Rivers riverine	Swim on side with flipper sometimes dragging along bottom. Average swimming speed ~3 kt	fish (<30 cm) and crustaceans (shrimp)	Habitat is muddy with minimal visibility. Hunt singly or in small groups (2-10 animals)	Walker 1968 Herald et al. 1969 Pilleri 1970
Platanista indi	20-225 kg	Ganges, Indus, and Brahmaputra Rivers riverine	Swim on side with flipper sometimes dragging along bottom. Average swimming speed ~3 kt	fish (<30 cm) and crustaceans (shrimp)	Habitat is muddy with minimal visibility. Hunt singly or in small groups (2-10 animals)	Walker 1968 Herald et al. 1969 Pilleri 1970
Pseudorca crassidens	1400 kg	pelagic		cephalopods and fish	Feed in groups of several hundred animals	Walker 1968

V
HABITAT/PREY/BIOLOGY

SPECIES	SIZE	HABITAT	BEHAVIOR	PREY	REMARKS	REFERENCES
Stenella sp.	to 165 kg	pelagic	Hunt (feed) near surfaces	fish	Occur in schools of a few to several hundred animals	Walker 1968 Leatherwood, Evans, Rice 1972
Tursiops truncatus (Montagu)	150-200 kg	bays and inshore waters littoral and sometimes riverine	Tilts head downward and scans laterally over 25°-30° arc or with a circular motion while echolocating	fish (most abundant species), sharks, shrimp, rays, squid		Norris et al. 1961 Evans and Prescott 1962 Walker 1968

APPENDIX IV

BIBLIOGRAPHY OF ACCUMULATED LITERATURE FOR BATS

LISTING FORMAT

LANGUAGE

6-DIGIT CODE		ORIGINAL	TRANSLATION
AUTHOR(S)	YEAR OF ISSUE		
TITLE OR DESCRIPTION			
SOURCE			

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KEY TO 6-DIGIT NUMBER CODE

DIGITS

1	2	3	4	5	6

DIGIT(S)	FUNCTION(S)
1	ORDER
	1 CETACEA
	2 CHIROPTERA
	4 OTHER
2-3	ECHOLOCATION
	1 DETECTION
	2 DISCRIMINATION
	10 PERFORMANCE
	20 SIGNALS ; FORMAT
	40 BEHAVIOR
4-5	BIOLOGY
	1 MORPHOLOGY ; ANATOMY
	2 AUDIOMETRY
	4 SIGNAL PROCESSING, CONDITIONING
	10 SOUND GENERATION
	20 SOUND RECEPTION
6	ECOLOGY
	1 HABITAT
	2 PREY

Examples:

231210 *A report about bats (2). Includes measurements, description, or commentary about echolocation signals (e.g., characteristics, repetition rate) (20), and the bats' performance (10) on target or obstacle detection or avoidance (1) (20+10+1=31), plus measurements, description or commentary on the bats' ability or capability to detect and/or localize sounds (echoes) (20), and the morphology and/or anatomy of the hearing organ (1) (20+1=21). Does not include information about the bats' normal hunting habitat or food prey (0).*

572101 *A report about whales, dolphins, or porpoises (1), including measurements and/or commentary on other animal forms (4) (4+1=5). Includes measurements, description, or commentary about the animals' echolocation signals (20), and their performance(s) (10) in discriminating between targets (2), plus commentary on the animals' behavior while echolocating (e.g., scanning motions, swimming speed) (40) (40+20+10+2=72). Includes commentary on the mechanics of sound generation (e.g., beaming, energy requirements) (10), plus description of the animals' normal hunting habitat(s) (1).*

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APPENDIX V

BIBLIOGRAPHY OF ACCUMULATED LITERATURE FOR WHALES, DOLPHINS, AND PORPOISES

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LISTING FORMAT

			LANGUAGE	
6-DIGIT CODE			ORIGINAL	TRANSLATION
	AUTHOR(S)	YEAR OF ISSUE		
	TITLE OR DESCRIPTION			
	SOURCE			

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KEY TO 6-DIGIT NUMBER CODE

DIGITS

1	2	3	4	5	6

DIGIT(S)	FUNCTION(S)
1	ORDER
	1 CETACEA
	2 CHIROPTERA
	4 OTHER
2-3	ECHOLOCATION
	1 DETECTION
	2 DISCRIMINATION
	10 PERFORMANCE
	20 SIGNALS ; FORMAT
	40 BEHAVIOR
4-5	BIOLOGY
	1 MORPHOLOGY ; ANATOMY
	2 AUDIOMETRY
	4 SIGNAL PROCESSING, CONDITIONING
	10 SOUND GENERATION
	20 SOUND RECEPTION
6	ECOLOGY
	1 HABITAT
	2 PREY

Examples:

231210 *A report about bats (2). Includes measurements, description, or commentary about echolocation signals (e.g., characteristics, repetition rate) (20), and the bats' performance (10) on target or obstacle detection or avoidance (1) (20+10+1=31), plus measurements, description or commentary on the bats' ability or capability to detect and/or localize sounds (echoes) (20), and the morphology and/or anatomy of the hearing organ (1) (20+1=21). Does not include information about the bats' normal hunting habitat or food prey (0).*

572101 *A report about whales, dolphins, or porpoises (1), including measurements and/or commentary on other animal forms (4) (4+1=5). Includes measurements, description, or commentary about the animals' echolocation signals (20), and their performance(s) (10) in discriminating between targets (2), plus commentary on the animals' behavior while echolocating (e.g., scanning motions, swimming speed) (40) (40+20+10+2=72). Includes commentary on the mechanics of sound generation (e.g., beaming, energy requirements) (10), plus description of the animals' normal hunting habitat(s) (1).*

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APPENDIX VI

BIBLIOGRAPHY OF ACCUMULATED LITERATURE FOR OTHER ANIMALS

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LISTING FORMAT

LANGUAGE

$\boxed{\text{6-DIGIT CODE}}$ $\boxed{\text{ORIGINAL}}$ $\boxed{\text{TRANSLATION}}$

$\boxed{\text{AUTHOR(S)}}$ $\boxed{\text{YEAR OF ISSUE}}$

$\boxed{\text{TITLE OR DESCRIPTION}}$

$\boxed{\text{SOURCE}}$

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KEY TO 6-DIGIT NUMBER CODE

DIGITS					
1	2	3	4	5	6

DIGIT(S)	FUNCTION(S)
1	ORDER
	1 CETACEA
	2 CHIROPTERA
	4 OTHER
2-3	ECHOLOCATION
	1 DETECTION
	2 DISCRIMINATION
	10 PERFORMANCE
	20 SIGNALS ; FORMAT
	40 BEHAVIOR
4-5	BIOLOGY
	1 MORPHOLOGY ; ANATOMY
	2 AUDIOMETRY
	4 SIGNAL PROCESSING, CONDITIONING
	10 SOUND GENERATION
	20 SOUND RECEPTION
6	ECOLOGY
	1 HABITAT
	2 PREY

Examples:

231210 A report about bats (2). Includes measurements, description, or commentary about echolocation signals (e.g., characteristics, repetition rate) (20), and the bats' performance (10) on target or obstacle detection or avoidance (1) (20+10+1=31), plus measurements, description or commentary on the bats' ability or capability to detect and/or localize sounds (echoes) (20), and the morphology and/or anatomy of the hearing organ (1) (20+1=21). Does not include information about the bats' normal hunting habitat or food prey (0).

572101 A report about whales, dolphins, or porpoises (1), including measurements and/or commentary on other animal forms (4) (4+1=5). Includes measurements, description, or commentary about the animals' echolocation signals (20), and their performance(s) (10) in discriminating between targets (2), plus commentary on the animals' behavior while echolocating (e.g., scanning motions, swimming speed) (40) (40+20+10+2=72). Includes commentary on the mechanics of sound generation (e.g., beaming, energy requirements) (10), plus description of the animals' normal hunting habitat(s) (1).

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